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Impacts of climate-mediated vegetation shifts and regional climate change on coastal avian community dynamics across the Gulf of Mexico

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Impacts of climate-mediated vegetation shifts and regional climate change on coastal avian community dynamics across the Gulf of Mexico

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Dedication

This work is dedicated to my friends and family that have been a constant source of support and encouragement throughout my academic journey. To my cohort: Ben, Maggie, and Cody, who have been my home away from home along this journey. To my amazing parents and brothers, Kimberly, Richard, Kyle, Kevin, and Peggy for your unconditional support and love. Thank you all for everything you do for me. Finally, to a special person whose support comes from peaceful and distant places, Jeff, thank you for all of the guidance and love throughout my life.

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Abstract

Impacts of climate-mediated vegetation shifts and regional climate change on coastal avian community dynamics across the Gulf of Mexico

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Climate change is considered to be a major threat to extant biodiversity. In addition to direct impacts of changing climatic conditions, poleward shifts in foundation species associated with warming temperatures may exacerbate impacts on higher trophic level species by altering habitat structure and resource availability. Across the Gulf of Mexico (GoM) reductions in severity and duration of winter freezes have facilitated the expansion of mangroves into previously salt marsh dominated habitat. Using birds as model taxa, I investigated the impacts of climate-mediated shifts in foundational species on multiple facets of avian biodiversity. I paired a long-term, standardized avian monitoring dataset (e.g. U.S. Geological Survey Breeding Bird Count) with environmental variables to investigate drivers of avian biodiversity change along coastal sites throughout the GoM and eastern portion of Florida from 1980-2017. Specifically, I was interested in testing whether expansion of mangrove-dominated wetlands and changes in regional climate change (i.e. temperature and precipitation) drive shifts in bird

species richness (α-diversity) or elevated rates of bird community turnover through time (temporal β-diversity). I documented changes in α-diversity and temporal β-diversity in both total and wetland bird communities across the GoM. Increases in mangrove cover at fine-spatial scales predicted changes in α-diversity and temporal β-diversity, whereas, coarse-scale changes in temporal β-diversity were predicted by climate. Increasing prevalence of southerly species were associated with faster rates of warming and increased temporal β-diversity, indicating potential poleward shifts in species ranges may be one factor underlying biodiversity change. Modifications in microclimate, biotic interactions, and resource availability associated with mangrove expansion may underlie observed shifts in bird biodiversity. My findings suggest that climate-mediated shifts in foundation species are likely impacting biodiversity of higher trophic level species and may exacerbate biodiversity change driven by the direct impacts of altered temperature and precipitation regimes. As mangrove habitats are predicted to continue to expand across the GoM, integrating data on in foundation species will be crucial for future assessments and adaptive management of climate-mediated changes in avian biodiversity.

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Introduction

Global biodiversity has been declining at rates higher than expected background extinction rates (Dirzo et al., 2014). Understanding changes in biodiversity is critical as maintenance of extant biodiversity promotes ecosystem function (Cardinale et al., 2006; Hector and Bagchi, 2007), stabilizes ecosystems (Tilman and Downing, 1994; Tilman, 1996), and supports human well-being (Pecl et al., 2017). Changes in biodiversity have been linked to a myriad of natural, stochastic, and anthropogenic processes that operate on different spatiotemporal scales (Ceballos et al., 2015; Jarzyna and Jetz, 2018). Though contemporary loss of global biodiversity has been largely attributed to changes in land use land cover (LULC; Newbold et al., 2015; Northrup et al., 2019), it is widely recognized that climate change has also manifested in species-specific and community-wide ecological shifts (Parmesan & Yohe, 2003). Thus, understanding how climate change may interact with other drivers of biodiversity is becoming increasingly crucial for scientists to predict local, regional, and global shifts in community structure and effectively conserve extant ecosystems.

Changes in climate can impact ecological communities in a variety of ways. At the species level, climate change may cause shifts in species ranges (Parmesan et al., 1999; La Sorte and Thompson, 2007), alterations in individual phenology (Visser et al., 2006; Socolar et al., 2017), and changes in species abundances (Northrup et al., 2019). Novel species assemblages can also result from climate-mediated shifts (Chapin and

Starfield, 1997), and this may lead to altered biotic interactions, such as phenological mismatch among plants and pollinators (Harrington et al., 1999) or new predator-prey interactions (Harley, 2011). These altered interactions may lead to further shifts in biodiversity beyond those predicted based on single-species models.

Climate-mediated range shifts of foundation species have the potential to be a major driver of biodiversity due to their disproportionate impact on biotic interactions and environmental conditions (Ellison et al., 2005; Sorte et al., 2017). The woody encroachment phenomenon is one example of a climate-mediated shift in land cover, where historically herbaceous-dominated systems transition to woody-dominated, which can influence the assembly and persistence of higher trophic species (Pidgeon et al., 2001; Sirami et al., 2009; Stanton et al., 2018). Woody encroachment has been documented across a geographically diverse subset of ecosystems, from interior grassland prairies to coastal wetlands (Stevens et al., 2017; Saintilan et al., 2014; Osland et al., 2013; Osland et al., 2017). Though ecological processes driving encroachment of woody vegetation are system-dependent, generally the ecotonal state is characterized by an increase in structural complexity and heterogeneity which increases exploitable niche space (Bazzaz, 1975). As woody encroachment continues, these ecotones will become increasingly dominated by woody plants and are expected to support distinct species assemblages relative to the historic community (Baker et al., 2002).

Wetland ecosystems of the Gulf of Mexico (GoM) may be especially sensitive to climate-mediated range shifts as they encompass the range boundary between woody mangrove-dominated wetlands in the south and herbaceous salt marsh-dominated

wetlands in the north (Guo et al., 2013; Armitage et al., 2015). Previous studies have documented an expansion of black mangroves (*Avicennia germinans*) into previously salt marsh dominated (*Spartina alterniflora*) habitat, associated with decreases in winter freezes (Osland et al., 2013; Armitage et al., 2015). Studies focused along the marsh – mangrove ecotone have found that salt marsh grasses and mangrove trees provide drastically different forms of habitat and are associated with divergent sets of benthic, nekton, and insect communities (Feng et al., 2014; Smee et al., 2017; Scheffel et al., 2018; Loveless and Smee, 2018). Therefore, coastal sites across the GoM provide ample opportunity for investigating the community-wide impacts of climate-mediated woody encroachment on biodiversity.

Birds are an excellent model taxon for understanding how shifts in foundation species impact higher trophic levels because of their diversity in trophic positions, connection to terrestrial and aquatic ecosystems, and high mobility allow for observable, rapid responses to changes in habitat. Additionally, it has been well-documented that bird distributions are governed by various vegetation characteristics, such as structural complexity and floristics (MacArthur & MacArthur, 1965; Fleishman et al., 2003; Sirami et al., 2009). Beyond the intrinsic properties that make birds reliable model taxa, birds are experiencing notable shifts in species distributions (LaSorte and Thompson, 2007; La Sorte and Jetz, 2012), species abundances (Northrup et al., 2018), and community composition (Tingley and Beissinger, 2013; Princé and Zuckerberg, 2015; Jarzyna and Jetz, 2017). Research has shown that across North America avian communities are undergoing a high degree of community turnover at the taxonomic, functional, and

phylogenetic levels (Jarzyna and Jetz, 2017). While past analyses have identified synergistic impacts of climate and LULC change on avian communities, these analyses were either constrained to a subset of avian communities (Jarzyna et al., 2016; Northrup et al., 2019) or did not consider community responses to climate-driven shifts in foundation species.

Here, I used a combination of long-term, standardized avian point count surveys (i.e. USGS Breeding Bird Survey) and remotely sensed environmental variables to investigate the impacts of climate change and mangrove expansion on coastal avian communities across the GoM and the eastern coast of Florida. First, I used baseline data to evaluate spatial differences in community composition associated with coastal wetlands to test the hypothesis that there are distinct avian assemblages associated with mangrove-dominated and marsh-dominated wetland sites (**H1**). Second, I quantified time-series trends in avian α- and temporal β-diversity and investigated the importance of key land cover and climate drivers in predicting changes in biodiversity components across the region. I predicted that sites that experienced the greatest rates of change in wetland habitat cover (e.g., mangrove expansion) and climate (temperature and precipitation) would correspond to greater changes in α-diversity and temporal β-diversity **(H2)**. Third, I evaluated whether poleward range expansions of avian species may be a key driver of temporal β-diversity across sites, and I predicted that avian communities will become increasingly dominated by more southerly species over time which will drive increases in temporal β-diversity **(H3)**.

Methods

Data Collection and Processing

Avian community data was extracted from the North American Breeding Bird Survey (BBS; http://www.pwrc.usgs.gov/). The BBS is a standardized, long-term dataset that records all detections and abundances of breeding birds across Mexico, Canada and the United States along ~4000 predefined routes (Pardiek et al., 2019). Surveys are conducted by skilled volunteers once a year between late May to early July, corresponding with peak breeding season for most North American birds. All birds detected are recorded (via auditory and/or visual detections) every 0.8-km within a ~0.4-km radius from the route for 50 three-minute point counts (Sauer and Link, 2011). I restricted my analysis to routes that were situated in coastal areas across the GoM and eastern Florida from 1980 to 2017, which corresponded to years for which LULC data was available. Prior to 1997, BBS survey results were aggregated across the 50 point counts at intervals of 10 points, creating five counts of bird occurrences and abundance for each route. I termed each aggregated count a "segment", with five segments per route. I used this segment data to analyze fine-scale spatial patterns in bird communities in addition to coarser route-level patterns. Additionally, using the Land Condition Trend Analysis (LCTA; Schreiber and Whitworth, 1998) database, I created a "wetland bird" dataset from the total dataset to assign species as wetland-associated by selecting species that were described as "swamp/marsh," "coastal," and/or "shoreline." Both total and wetland bird biodiversity were investigated in all analyses.

LULC data was gathered from the National Land Cover Database (NLCD) which was collected by the Multi-Resolution Land Characteristics Consortium, National Oceanic and Atmospheric Administration Coastal Change Analysis Program (C-CAP), and the United States Geological Survey classified mangrove data (Giri et al., 2011, Giri unpublished data). All LULC data sources were produced as 30-m resolution classified maps ensuring consistent resolution was attained during data extraction. Classified land cover maps across datasets were reclassified in ArcGIS 10.6 to create standardized LULC classes for all routes. Reclassified land cover classes used for analysis included emergent wetlands, (e.g. salt marsh and other herbaceous wetlands), woody wetlands, urban, agriculture, upland grasslands, forest, bare land, and open water. Since mangrove was not distinguished from other woody wetland classes in the NLCD or C-CAP datasets, I used mangrove specific classified imagery to provide an additional mangrove land cover class (Giri et al., 2011). Because areas classified as woody wetlands where mangrove occur could encompass both non-mangrove (e.g., cypress swamps) and mangrove habitat, I subtracted mangrove cover from woody wetland cover to create a non-mangrove woody wetland class. LULC data was extracted from 0.4-km buffers extending around digitized bird survey routes. A 0.4-km buffer size around the route was chosen because it corresponds to the limit at which observers are permitted to record birds. The buffered routes were then sub-divided into five, equal-sized segments to correspond with the spatial resolution at which the bird count data was consistently reported as described above. To ensure I was investigating changes in primarily wetland bird communities, I

further restricted my analyses to route-segments that had a minimum 20% wetland cover at least one point within the time-series.

Climate data was extracted from the 4-km resolution PRISM Climate Group dataset which includes monthly mean temperature and precipitation from 1975 to 2017 (Oregon State University; http://prism.oregonstate.edu/). I used the coordinates from the centroid of each segment to extract data from the rasterized climate data. I extracted monthly climate data for the entire time series plus five years prior to the start of the time series for each segment. Minimum, maximum and mean monthly temperature for each meteorological season (winter, spring, summer, fall) were calculated. Seasonal averages for temperature minima, maxima and means metrics were highly correlated, however, so I focused on seasonal means for the remainder of the analyses. Additionally, it is expected that changes in climate during the breeding season (March-August) will confer the greatest pressure on adult breeding birds and nestlings; therefore, I used the mean monthly temperature for the breeding season ($T_{breeding}$) in subsequent biodiversity analyses. States along the GoM follow precipitation regimes characterized by wet (May–October) and dry seasons (November–April). Thus, seasonal means for monthly precipitation were calculated for wet (p_{wet}) and dry (p_{dry}) in each year. Lastly, I estimated climate conditions for the start and end of each time series for each segment by calculating the average of each variable for that survey year and the four previous years, yielding 5-year averages of climate. Averaging the data this way accounts for potential climate extremes obscuring relationships and evidence suggests that bird species likely experience lag effects in their response to changing climate (Lemoine et al., 2007; La

Sorte and Jetz, 2012; Princé and Zuckerberg, 2015). Then, I subtracted the 5-year average for each climate variable at the start of the time series from the end of the time series to estimate the change (Δ) in climate conditions experienced at each segment across the years in which it was surveyed. For the route-level analysis, I averaged the climate variables extracted from each route centroid and summed the land cover extracted from buffers for segments retained based on wetland habitat cover to generate route-level predictors. I then calculated total change in each route-level predictor across each time series as described above.

MULTISPECIES OCCUPANCY MODEL

Animals are seldom detected perfectly during sampling efforts. For example, cryptic birds that rarely sing or hide in thick understory may be wrongfully classified as absent. Thus, ignoring imperfect detection can result in erroneous estimates of biodiversity metrics (Tingley and Beissinger, 2013; Iknayan et al., 2014). I used a multispecies occupancy model that accounts for imperfect detection to estimate true occupancy for bird species across the selected BBS surveys (Dorazio et al. 2010; Lele et al. 2012; Peach et al., 2017). Traditional occupancy models rely on a "robust design" where repeated "secondary" visits within a "primary" season are used to estimate detection. However, BBS routes are sampled only once annually using point counts, spaced every 0.8-km along each of five segments, with counts of species detected, recorded only at the segment-level prior to 1997. I used single-survey extensions of occupancy models to estimate occupancy and detection from single-visit

"secondary" surveys by using information from relevant predictors and multiple annual surveys (1980-2017) of BBS routes (Lele et al., 2012; Peach et al., 2017). The multispecies occupancy model was fit under a Bayesian framework using the program JAGS (Just Another Gibbs Sampler; http://mcmc-jagssourceforge.net/) via R (R Core Team, 2019) with the package 'rjags' (Plummer, 2019).

The multiple species occupancy model had two sub-models: (1) an observation sub-model that accounts for imperfect detection using single primary surveys and relevant predictors (Lele et al., 2012; Peach et al., 2017), and (2) an ecological sub-model that estimates true occupancy and provides annual estimates of richness, while accounting for undetected species via data augmentation (Royle et al. 2007; Guillerta-Arroita et al. 2019). In the observation sub-model, observed occupancy of species *i* at segment *j* for year *t*, $y_{i,j,t}$, was conditional on true occupancy, $z_{i,j,t}$, and related to detection probability, $p_{i,j,t}$, through a Bernoulli process as follows (eqn.1):

$$y_{i,j,t}|z_{i,j,t} \sim Bernoulli(z_{i,j,t} * p_{i,j,t}) \quad (1)$$

Detection probability was in turn related to predictors thought to influence species detection including first-year "observer effects" (Sauer et al., 1994), day of year (Tingley and Beissinger, 2013), time of day, and a species' phylogenetic relatedness (Sólymos et al., 2018), using a logit function (eqn. 2):

$$logit(p_{i,j,t}) = a_0 + a_1 * (observer)_{r,t} + a_2 * (day\ of year)_{r,t} + a_3 * (time\ of\ day)_{j,t} + \delta_s (2)$$

where α_0 represents the intercept, estimated to represent mean detection on the logit scale (eqn. 3),

$$\alpha_0 = \log\left(\frac{\mu_{p,0}}{1-\mu_{p,0}}\right) \quad (3)$$

and was given slightly informative priors: $\mu_{p,0} \sim Beta(4,4)$. The $\alpha_{1\text{-}3}$ are the fixed community-level coefficients related to each predictor and were given uninformative, Normal priors: $\alpha_{1\text{-}3} \sim$Normal(0, 10). Note that the observer effect and day of year were both recorded at the route level, *r*, every year. All species were grouped into parsimonious phylogenetic groups at the order and family level by visually inspecting a consensus tree with all species detected in the time-series generated from BirdTree.org (Jetz et al., 2012; Jetz et al., 2014). Passeriformes comprised all songbird species in my dataset (~46% of total species) and were thus subdivided into the appropriate lower family classification. Previous work suggests that phylogenetic relatedness is indicative of species-level detection properties (e.g. singing rate) that can be useful when allowing species to borrow strength across group means (Sólymos et al., 2018). This approach allowed rare species to borrow data from more common species belonging to the same phylogenetic group and facilitate estimates of their detection and occupancy that would not be possible via single-species models alone (Dorazio et al. 2010). The effect of individual species within a phylogenetic group was represented in the detection sub model as δ_s, where the random intercept of species *s* is given an uninformative Normal prior: $\delta_s \sim$ Normal(0, 6).

The ecological sub-model estimates true occurrence for detected and undetected species within the community by augmenting the number of detected species in a given segment and year, $ND_{j,t}$, by the number of undetected species that could have been

present, $NU_{BCR[j]}$. This number was defined as the total number of species detected for all segments within the Bird Conservation Region (BCR). The BCR is an ecologically distinct regions determined by the North American Bird Conservation Initiative (Bird Studies Canada and NABCI, 2014; Royle et al., 2007; Dorazio et al. 2010). The use of BCR for data augmentation restricted the species pool based on their distributional and ecological constraints (i.e. detection of species endemic to Peninsular Florida are not estimated to occur in Gulf Coast Plains route). The true occupancy, $z_{i,j,t}$, for each species, in each segment, and year were then the outcome of a Bernoulli process including the probability of occupancy, $\psi_{i,j,t}$ and an indicator, $w_{i,j,t}$, of whether the species was likely present in that segment that year (eqn. 4):

$$z_{i,j,t} \sim Bern(w_{i,j,t} * \psi_{i,j,t}) \quad (4)$$

Detected species from $ND_{j,t}$ were assigned $w_{i,j,t}$ =1, and undetected species from $NU_{j,t}$ were assigned as present or absent based on $w_{i,j,t}$ ~Bern(0.5). Bird richness became a derived parameter defined as (eqn. 5):

$$NT_{j,t} = \sum_{i=1}^{I} (z_{i,j,t}). \quad (5)$$

The probability of occupancy, $\psi_{i,j,t}$, was related to random intercepts for route and year using a logit link function to account for spatial autocorrelation among segments belonging to the same route, and the repeated measures sampling design (eqn. 6):

$$logit(\psi_{i.j}) = \beta_0 + \varepsilon_r + \varepsilon_t \quad (6)$$

where β_0 is the intercept, representing mean occupancy on the logit scale (eqn. 7),

$$\beta_0 = \log\left(\frac{\mu_{\psi,0}}{1-\mu_{\psi,0}}\right) \quad (7)$$

and were given slightly informative priors: $\mu_{\psi,0} \sim Beta(4,4)$. Random intercepts were given uninformative Normal priors: ε_r ~Normal(0, 10) and ε_t ~Normal(0, 10).

BIODIVERSITY METRICS AND COMMUNITY MEAN RANGE LIMIT

To understand temporal changes in avian biodiversity across the Gulf of Mexico, I quantified changes in α-diversity (local species richness) and temporal β-diversity (community turnover). When paired together these indices provide a more holistic understanding of shifts in biodiversity by evaluating changes in the total number of species as well as the shifts in community composition (McGill et al., 2015). My analyses focused on the start and end point of each survey to capture total change across the time-series for each segment. Diversity indices were calculated using detection-corrected estimates by using the mean values of $z_{i,j,t}$ from all MCMC runs such that if mean $z_{i,j,t} > 0.5$ then $z_{i,j,t} = 1$ (Benoit et al., 2018). The α-diversity was directly calculated from the occupancy model as the sum of all species estimated true occurrences for each year (eqn. 8).

$$\alpha\text{-diversity}_{j,t} = \sum_{i=1}^{I}\left(z_{i,j,t}\right) \quad (8)$$

where α-diversity for segment, *j*, at year, *t*, is the sum of all species *i* estimated true occurrences in the community. Relative changes in α-diversity across the time-series were quantified for each segment, *j*, as the difference between α-diversity in the final year, t_f, from the baseline year, t_0, divided by the α-diversity in t_0 (eqn. 9).

$$\Delta a\text{-}diversity_j = \frac{\alpha\text{-}diversity_{t_f,j} - \alpha\text{-}diversity_{t_0,j}}{\alpha\text{-}diversity_{t_0,j}} \quad (9)$$

Temporal β-diversity was calculated as the difference in community composition of segment, *j*, from the baseline year, t_0, and final survey year, t_f, using the Jaccard index (Jaccard, 1912) in the R package 'betapart' (Baselga and Orme, 2012). Jaccard's index is a robust similarity metric that quantifies the intersection of species present between two points in time or space. β-diversity may be driven by two separate processes governing overall changes in community composition: turnover and nestedness. Turnover is comprised of species replacement that does not result in the loss or gain of species, and nestedness is related to gains or losses of species where the species-poor community is a subset of the species-rich community (Baselga, 2010; Legendre, 2014). I calculated Jaccard's dissimilarity coefficient for each segment as follows (eqn. 10):

$$\beta_{Jac,j} = \beta_{Turn,j} + \beta_{Nest,j} = \frac{b+c}{a+b+c} = \frac{2b}{2b+a} + \left(\frac{c-b}{a+b+c}\right)\left(\frac{a}{2b+a}\right) \quad (10)$$

where *a* is the total number of species shared between the start and end points for segment, *j*, *b* is total number of the species that are present at segment, *j*, at the baseline year, t_0, but absent at the final year, t_f, and *c* is the total number of species that are absent at segment, *j*, at the baseline year, t_0, but present in the final year, t_f. As temporal β-diversity seemed to be driven primarily by differences in turnover instead of nestedness (see Results), I focused only on total temporal β-diversity (β_{Jac}) for subsequent analyses.

To investigate the proposed increased prevalence of lower-latitude species associated with climate change, I utilized a metric I have termed the Community Mean Range Limit (CMRL). This metric is calculated by first estimating the historical

poleward latitudinal range limit of each species within the dataset based on observed occurrence across all ~4000 BBS routes across North America for the beginning of the time series in 1980. To buffer against potential irruption years or vagrancies, the range limit for each species was calculated as the mean annual maximum latitude across 5 years between 1980 and1984. To estimate community-level changes in lower vs. higher-latitude species, I averaged the northern range limit of each species observed within a given community to calculate the CMRL. Lower values of this metric indicate a community that is dominated by lower latitude, southerly (tropical) species while higher values indicate a community that is dominated by higher latitude, northerly (temperate) species. CMRL is less data intensive than existing metrics that rely on estimating a species thermal niche (e.g. Community Temperature Index (CTI)) (Devictor et al., 2008), making it more feasible for highly diverse datasets and incorporating shifts in species ranges due to direct temperate tracking as well as tracking of shifts in foundation species.

STATISTICAL ANALYSIS

First, I sought to determine whether there were differences in bird community composition associated with mangrove and emergent wetland habitat types. I used the 1980-1990 time period to test for differences in community structure across wetland land cover classes. This temporal range represents the baseline of the time series and includes a sufficient number of sites with mangrove cover to compare to emergent wetland sites. I averaged land cover and bird community data between 1980-1990 for each segment. I grouped segments into one of three wetland land cover classes: mangrove-dominated,

mangrove-present, or emergent. Sites where the ratio of mangrove to emergent wetland habitat cover was greater than 1 were deemed “mangrove-dominated”, sites where this ratio was between 0 and 1 were deemed “mangrove-present wetlands”, and sites with a 0 mangrove-emergent wetland ratio were “non-mangrove wetlands”. I calculated differences in bird community composition across segments using the Jaccard index. I used a non-metric dimensional scaling (NMDS) plot to graphically display differences in community composition across segments of varying wetland habitat types. I tested for statistical differences in community composition with Permutational Analysis of Variance (PERMANOVA; Anderson, 2001) with wetland habitat type treated as a fixed effect using the ‘adonis’ function in the R package ‘vegan’ (Oksanen et al., 2019).

Second, I evaluated overall trends in α-diversity and temporal β-diversity across the time series and compared mean trends for the total bird community and wetland bird communities using a series of two-sample *t*-tests. I evaluated whether mean trends in α-diversity for both total and wetland bird communities were different form zero using a series of one-sample *t* –tests. Temporal β-diversity is expected to increase over time based on ecological drift (Chesson and Warner, 1981; Dornales et al., 2014) and thus whether the mean slope differed from zero was not tested. I also compared spatial patterns in biodiversity across the four BCRs.

Third, I evaluated which climatic and land cover variables were most important in predicting relative change in α-diversity and temporal β-diversity of avian communities across the GoM. I conducted these analyses on data aggregated at two spatial scales: the segment and route levels. Due to the variability in the number of segments within routes

that met my criteria (i.e. ≥ 20% wetland land cover), between one and five segments per route were retained for the analysis. To assess whether wetland bird species responded to climate and land cover change differently than the total bird community, I ran separate models for biodiversity metrics calculated using the entire bird community and those calculated using wetland bird species in all subsequent analyses.

For assessment of fine-scale drivers of bird biodiversity change, I focused on segment-level estimates of relative change in α-diversity and temporal β-diversity. I used a linear mixed-effects model to identify predictors of relative change in α-diversity trends across segments. For the models in which temporal β-diversity was the response variable, it was not appropriate to use a linear model as Jaccard's dissimilarity index (β_{Jac}) is bound between zero and one, which violates assumptions of normal parametric statistical methods (i.e. constant variance; Cribari-Neto and Zeileis, 2010; Douma and Weedon, 2019). Thus, I modeled temporal β-diversity with a mixed-effect beta regression which is a type of generalized linear mixed-effects model (GLMM) that linearizes response variables using a logit-link function and assumes a beta distribution for the response variable. Fixed effects included in all models were based on *a priori* hypotheses related to important drivers of bird distributions and included change in mean temperature during the bird breeding season ($\Delta T_{breeding}$), change in precipitation during the wet season (Δp_{wet}) and dry season (Δp_{dry}), change in percent cover of mangrove (Δ mangrove), change in percent cover non-mangrove woody wetland (Δ non-mangrove woody wetland), change in percent cover of emergent wetland (Δ emergent wetland), change in percent cover in anthropogenic land cover classes (i.e. agriculture and urban; Δ anthropogenic),

and duration of each survey (Table 1). End-of-year species richness and segment time series duration were included as additional fixed effects (Table 1). To account for non-independence in observations among segments within a route, I included route as a random effect in all models. For temporal β-diversity models, because GLMMs do not assume constant error terms, I evaluated whether accounting for overdispersion of variance in temporal β-diversity as function of individual fixed effects improved model fit, and I selected overdispersion terms to be retained in the final model using likelihood-ratio test (Bayer and Cribari-Neto, 2016). Linear mixed-effects models were fit using the 'lme4' package (Bates et al., 2015) and mixed-effects beta regression models were fit using the 'glmmTMB' (Brooks et al., 2017) in R.

Since I expected differences in climate patterns to manifest primarily between routes as opposed to among segments within a route, and because patterns in biodiversity are often scale-dependent (Jarzyna et al., 2018), I ran another set of analyses with biodiversity metrics calculated at the route level using both the climate and LULC data. α- and temporal β-diversity indices were recalculated for pooled detection-corrected species occurrences for each route aggregated across only segments retained in the analysis based on wetland land cover. Multiple linear regression models were run for α-diversity and standard beta regression models were run for temporal β-diversity with climate and land cover variables described above included as fixed effects. As above, duration of route survey (years) and end species richness was included as an additional fixed effect in all models. Linear models were fit with the 'lm' function and beta

regression models were fit using the 'betareg' package in R (Cribari-Neto and Zeileis, 2010).

Finally, I evaluated the relationship of ΔCMRL through time with changes in climate and temporal beta diversity across routes. I expected CMRL to decrease the most at locations experiencing the most warming, and thus I modeled ΔCMRL as a function of change in mean spring temperature (ΔT_{Spring}) using a linear regression model. I used ΔT_{spring} in this instance because changes in spring temperatures have been shown to impact the number and proportion of both migratory and resident bird species (Lemoine & Böhning-Gaese, 2003). Additionally, I expected that ΔCMRL would be driven primarily by increases in southerly species which would drive negative associations between ΔCMRL and temporal β-diversity. Therefore, I utilized linear models to investigate the relationship between temporal β-diversity and ΔCMRL. I repeated this model for each component of temporal β-diversity (β_{Jac}, β_{Turn}, β_{Nest}) to investigate whether changes in community composition driven by ΔCMRL were manifested as species replacements, species loss/ gain, or both processes. Models for ΔCMRL were only run for the entire bird community because I had no *a priori* expectation that wetland bird communities would exhibit a differential response in northward expansion compared to the complete community.

Results

CHANGES IN AVIAN BIODIVERSITY OVER TIME

I analyzed 241 BBS route-segments and 73 BBS routes across the GoM from 1980 to 2017 to investigate the impacts of climate-mediated mangrove expansion and regional climate change on bird community composition (Fig. 1). Average route survey duration was ~23 years. Across the times series, 122,715 individuals belonging to 233 species of birds from 19 orders and 53 families were recorded. α-diversity was high for both total and wetland bird communities. Notably, α-diversity was higher at the route-level than the segment-level in both cases (total bird community: $mean_{segement}$ = 68 species, $mean_{route}$ = 79 species; wetland bird community: $mean_{segement}$ = 22 species, $mean_{route}$=27 species; Table 2). Estimates of relative change in α-diversity and temporal β-diversity were consistent between both segment and route-level scales (t = 1.79, df = 126.01, $p > 0.05$; t = 0.147, df = 127.29, $p > 0.1$), therefore, I will focus on overall biodiversity trends from the route-level analyses.

Across the time series, routes exhibited an average net loss in species richness for both total and wetland bird communities (Table 2). The total number of species lost for the total community on average was 2.1 species per route greater than that of wetland-associated species; however, there was no statistical difference in either absolute mean or relative change between both the total and wetland groups of birds (t = -1.66, df = 109.97, $p > 0.05$; t = 0.85, df = 111.41, $p > 0.1$). While the mean change in α-diversity across routes was less than zero for both total and wetland bird communities (t = -4.50, df = 72, $p < 0.001$; t = -4.91, df = 72, $p < 0.001$, respectively), the mean slope of the trend

only differed from zero for wetland birds (total: t = -1.46, df = 72, $p > 0.1$; wetland: $t = -2.00$, df = 72, $p < 0.05$). Total bird communities exhibited stronger declines in the eastern GoM, particularly along the northeastern portion of Florida, southern Florida, and near Port Charlotte (sites primarily located within the Peninsular Florida Bird Conservation Region; Fig. 2a,b). Conversely, trends in α-diversity for the western GoM (i.e. Texas) were more variable with some sites increasing in α-diversity while others declined (Fig. 2a and 3). Wetland bird communities follow similar patterns to those documented in the entire community with a steady decline in wetland bird species in Peninsular Florida (Fig. 2b). Routes within the other BCRs demonstrated variable temporal patterns in wetland bird α-diversity (Fig. 4).

Over the time-series, the total and wetland bird community experienced a mean change of 22% and 30% in community composition across routes, respectively, from the baseline year of each survey (Table 2). Temporal β-diversity was significantly higher for wetland bird species than the total bird community ($t = -3.77$, df = 109.14, $p < 0.001$). Approximately 63% of the change in total bird community composition (β_{Jac}) could be attributed to the turnover component (β_{Turn}) and the remaining 37% was attributed to nestedness (β_{Nest}). The nestedness component was higher for wetland bird species than total communities. Compared to the total community, the nestedness component was higher for wetland bird species; 53% and 47% of the change in the wetland bird community was driven by turnover and nestedness, respectively (Fig. 5a,b; Table 2). Total bird community temporal β-diversity was greatest at routes in southern Florida, southern Texas, and near the border of Texas and Louisiana (Fig 8a). Similar to α-

diversity, sites within Peninsular Florida demonstrated the strongest temporal trends (Fig. 6 and 7). Temporal β-diversity in wetland bird communities demonstrated similar patterns as described for the entire bird community (Fig. 8b)

SPATIAL PATTERNS IN COASTAL BIRD COMMUNITIES

Results from a spatial analysis of community structure from 1980 – 1990 suggest strong differences between both mangrove and emergent wetland bird communities (Fig. 9; PERMANOVA; *F*-statistic = 7.26, $R^2 = 0.07$, $p < 0.0001$, df = 2). Bird communities within mangrove-present wetland sites were intermediate between the two single-habitat wetlands site types, suggesting ecotonal communities represent a mix of bird species from both community types (Fig. 9).

LAND COVER AND CLIMATIC DRIVERS OF AVIAN BIODIVERSITY TRENDS

Regional climate exhibited expected long-term trends across sites within the study. Annual and breeding season temperature demonstrated linear increases from 1975 – 2017 for all temperature minima, maxima, and means variables (Fig. 10; Table 1). Additionally, p_{wet} increased over the study, whereas p_{dry} demonstrated a weak decline (Fig. 10). Land cover classes exhibited variable responses across the time series. Wetland cover classes (i.e. emergent wetland, non-mangrove woody wetland, and mangrove) all exhibited mean overall increases over the time series. Anthropogenic land cover (i.e. agriculture and urban) displayed variable patterns across routes driven generally by decreases in agricultural land cover and increases in urbanized land cover. Upland habitat

cover (i.e. grassland and forests) primarily decreased, with large reductions in forest cover and more minor losses in upland grassland habitat. (Fig. 11; Table 1).

In general, relative change in α-diversity was not well-predicted by climate or land cover variables at either the segment or route levels (Table 3 and 4). At the segment level, the total bird community model had better fit than the wetland bird community with marginal R^2 values of 0.27 and 0.11, respectively (Table 3). Only change in mangrove cover and species richness were important predictors of relative change in α-diversity across segments (Table 3). Relative change in α-diversity demonstrated a negative relationship with Δ mangrove percent cover for both total and wetland bird communities. Similarly, relative change in α-diversity demonstrated a negative relationship with both species richness and wetland bird species richness in the respective models. The random-effects components explained much of the residual variation in relative change in α-diversity (total R^2 conditional = 0.81, wetland R^2 conditional = 0.51, respectively.). This is not surprising given the high intraclass-correlation values and the expectation that many parameters would likely be highly correlated between segments within a route (Table 3).

Despite the large amount of variation in segment-level relative change in α-diversity explained by the random effect of route, route-level linear models also performed poorly with R^2 values of 0.19 and 0.12 for total and wetland bird communities, respectively (Table 4). At the route-level, none of the climate or land cover predictors were important in predicting relative change in alpha diversity. There was a weak

positive association between species richness and relative change in α-diversity for the total bird community.

For segment-level models of temporal β-diversity, generalized linear mixed-effects models were overall better fits for the data compared to models fit for changes in α-diversity, with marginal R^2 values of 0.45 and 0.54 for total and wetland bird communities, respectively. There were positive relationships between temporal β-diversity and Δ mangrove cover for both total and wetland bird communities indicating sites experiencing mangrove expansion are experiencing faster rates of change in community composition (Table 5). Similarly, Δp_{wet} exhibited a positive relationship with temporal β-diversity for both community types, indicating segments that are increasing in precipitation more are experiencing greater increases in temporal β-diversity. Similar to relative change in α-diversity, both community types demonstrated negative relationships between temporal β-diversity and species richness. Intuitively, temporal β-diversity for both community types demonstrated positive relationships between survey duration, as more community change is detected within longer time series (Table 5).

At the route-level, standard beta regression models for temporal β-diversity also had high overall model fits for both total and wetland community, with pseudo R^2 values of 0.65 and 0.69, respectively (Table 6). There was a positive relationship between Δ $T_{breeding}$ and temporal β-diversity for both community types indicating that sites that warmed more concurrently changed more in bird community composition. Seasonal precipitation patterns had differential effects on total and wetland bird temporal beta diversity. Δ p_{wet} was a strong predictor for wetland bird temporal β-diversity whereas Δ

p_{dry} was related to increases in total bird temporal β-diversity. Interestingly, total bird temporal β-diversity was related to increases in the amount of woody wetland within routes, signifying land cover relationships at the route-level undetected at the segment-level. Additionally, wetland bird temporal β-diversity was negatively associated with changes in anthropogenic cover, potentially due to restoration of habitat via conversion of agricultural land. Lastly, consistent negative relationships between species richness and temporal β-diversity were demonstrated at the route-level as well and a positive relationship between duration of survey and total bird temporal β-diversity (Table 6).

COMMUNITY MEAN RANGE LIMIT

Overall, CMRL decreased over time (median ΔCMRL = -0.26° change; Table 2), although there was considerable variation across routes, ranging from ΔCMRL -2.74° to ΔCMRL +0.86° (Table 2). Change in mean spring temperature was a strong predictor of ΔCMRL, where increases in spring mean temperatures predicted decreases in ΔCMRL (Fig. 12a; $R^2 = 0.17$, $p < 0.001$, df = 71; Table 7). This negative relationship suggests increases in temperature correspond to increased presence of southerly species. Temporal β-diversity (β_{Jac}) displayed a negative relationship with ΔCMRL (Fig. 12b; $R^2 = 0.11$, $p < 0.01$, df = 71; Table 7) where temporal β-diversity was highest at sites that were becoming dominated by southerly species. Furthermore, the turnover component of temporal β-diversity (β_{Turn}) exhibited a similar relationship with ΔCMRL (Fig. 12c; $R^2 = 0.07$, $p < 0.05$, df = 71; Table 7) whereas nestedness (β_{Nest}) exhibited no relationship with ΔCMRL (Fig. 12d; $R^2 = 0.01$, $p > 0.05$, df = 71; Table 7). This suggests changes in

community composition that are driven by ΔCMRL are mediated by species replacements rather than systematic losses and gains.

Discussion

Coastal avian bird communities across the GoM have undergone changes in species richness and community composition, which appear to be linked to mangrove encroachment and changes in regional climate. Biodiversity change was largely driven by changes in temporal β-diversity. Changes in α-diversity were not as well predicted by changes in climate or land cover across sites used in the current study. Strong localized effects of mangrove expansion on changes in biodiversity met predictions based on historical spatial patterns in avian community composition as distinct bird community types were found between mangrove and emergent marsh-dominated wetlands. Associations between temporal β-diversity and ΔCMRL also suggest that changes in communities were partially driven by shifts in community composition toward more southerly species. This pattern is expected if species are shifting their ranges poleward as temperature increases. Notably, predictors of change in avian biodiversity were found to be scale-dependent, with mangrove land cover coming out as most important in the finer-scale, segment-level models and temperature and precipitation being more important in coarser-scale, route-level models. Thus, climate change may be altering selective filters on avian community assembly through both changes in habitat at local scales and climate regime shifts at regional scales.

At finer-spatial scales, mangrove expansion was a strong predictor for increases in temporal β-diversity in both total and wetland bird communities, likely due to shifts in resource availability and changes in abiotic conditions associated with mangrove encroachment. Increases in mangrove prevalence has been demonstrated to shift

abundance and diversity of both aquatic and insect prey resources for birds (Loveless and Smee, 2017; Diskin and Smee, 2017; Scheffel et al., 2018). For example, Scheffel et al. (2018) demonstrated higher density of infauna at marsh sites when compared to mangrove sites. Likewise, higher mangrove cover was found to correspond to decreased abundance and diversity of insect communities relative to sites dominated by emergent marsh (Loveless and Smee, 2017). Thus, mangrove encroachment may select against insectivorous birds and infaunal feeders while promoting water-column feeding species. Furthermore, the increased structural complexity of mangrove trees may alter predator-prey interactions or foraging success of bird species, further shifting community composition. Additionally, mangrove expansion into salt marshes may lead to shifts in microclimate, which may exert an additional selective filter on bird community composition (Frey et al., 2016). Specifically, the structure of mangrove trees leads to reductions in wind speeds and accompanying increases in both aboveground and soil surface temperature relative to emergent marsh habitat (Guo et al., 2017), which may favor species that are aerial insectivores that benefit from reduced wind speeds (Møller, 2013) or have warmer thermal preferences (Frey et al., 2016). Moreover, mangrove expansion may also be impacting bird community structure by redistributing available nesting habitats. Mangrove stands provide roosting areas for many birds (e.g. Great Egret, Northern Waterthrush), likely due to reductions in predation, reduced distance to foraging grounds, and potential thermoregulatory benefits associated with the woody structure relative to herbaceous habitats (Beauchamp, 1999; Smith et al., 2009; Jonhston-González and Abril, 2019). Marsh specialist species (e.g. Seaside sparrow; Greenberg et

al., 2006; Correll et al., 2016), will likely lose nesting habitats as mangroves expand, as they are typically ground nesters and use marsh grasses as nesting material (Greenberg et al., 2006). Thus, shifts in biotic and abiotic conditions as mangroves expand will provide novel niche space for a divergent subset of bird species, while selectively excluding salt marsh specialists.

Changes in mangrove cover was also an important predictor of relative change in α-diversity, as increasing mangrove cover resulted in declines in α-diversity over time. This negative relationship between relative change in α-diversity and mangrove cover change seemed to contrast with the idea that structural complexity should increase diversity through the creation of novel niche space (MacArthur and MacArthur, 1961). While mangrove habitats are more structurally complex than emergent marshes due to their woody and vertically complex features, they are relatively depauperate of other wetland plant species, compared to their mixed-marsh counterparts (Guo et al., 2017). Thus, higher floristic diversity associated with emergent marsh habitats could be driving higher alpha diversity of birds, as past studies have linked bird species richness with plant species diversity (Rotenberry, 1985; Rahbek and Graves., 2001). Conversely, mangrove encroachment may be driving habitat homogenization at landscape scales, as most mangrove cover increases detected in this study represented expansion of existing mangrove stands rather than novel colonization. More high resolution and replicated studies at ecotonal boundaries may be able to parse out the effects of habitat turnover versus habitat complimentary on changes in bird α-diversity associated with mangrove encroachment.

Significant influences of climate and diminished strength of land cover predictors on temporal β-diversity at a coarser spatial scale suggests impacts of climate may be scale-dependent. This finding is consistent with previous research demonstrating that changes in land cover were most important in driving shifts in biodiversity at fine-scales (Newbold et al., 2015), while changes in climate have the strongest influence on bird community composition at regional scales (Princé and Zuckerberg, 2015). Community responses to changes in temperature are likely complex, suspected to be mediated by changes in competition (Alexander et al., 2015; Kubelka et al., 2016), resource availability (Bale et al., 2002; Winkler et al., 2013), and physiological limitations (Webb, 1987; Albright et al., 2017). The importance of $\Delta T_{breeding}$ in route-level models indicates that communities may be changing in response to climatological pressures on breeding success, such as increases in nest predation rates by ectotherms mediated through increases in temperature (Zuckerberg et al., 2018). For example, in using individual-based models of bird nest predation rates by ratsnakes, DeGregorio et al. (2015) demonstrated that increases in spring temperatures of 0.5°C corresponded to increases in nocturnal predation rates of 7% and increases by 2°C led to increases of nocturnal nest predation rates in March of nearly 2005. I documented changes in breeding season temperatures of a similar magnitude (average change of 0.46°C with maximum changes of 1.38°C), suggesting that increases in predation rates may partially explain patterns in community turnover relative to increasing breeding season temperatures. Furthermore, the influence of temperature on temporal β-diversity was likely partially driven by redistribution of southerly and northerly-associated species assemblages, as demonstrated

via relationships between temporal β-diversity, CMRL, and change in mean spring temperature. Princé and Zuckerberg (2015) documented similar increases in the dominance of warm-associated species using two similar metrics to CMRL, the Community Temperature Index (CTI) and an abundance weighted form of CTI (Devictor et al., 2008), for bird communities in the eastern U.S. These shifts in community composition toward species historically found at lower latitudes are likely driven by species replacements at the dynamic edges of species ranges as northerly species may shift their southern ranges poleward (Zuckerberg et al., 2009) and southerly species expand their northerly range limits (Thomas and Lennon, 1999).

Though most of the research in avian responses to climate change have been attributed to changes in temperature (Thomas et al., 2004; Hitch and Leberg, 2007; Chen et al., 2011), precipitation is increasingly being recognized as another strong driver of bird distributions (Tingley et al., 2012; Illán et al., 2014). Future trends in precipitation change across the GoM are much less certain than that of temperature, with climate models predicting that precipitation will exhibit higher spatial heterogeneity in the future (Biasutti et al., 2012). Precipitation was a significant predictor of temporal β-diversity in the current study, possibly related to changes in prey-availability (Carroll et al., 2011) and nesting success (Zuckerberg et al., 2018) associated with altered precipitation regimes. Differential responses of total and wetland bird temporal β-diversity to changes in seasonal mean precipitation suggest that altered precipitation may impact wetland birds differently from other taxa. For example, wetland species may have shown greater sensitivity to precipitation during the wet season because they utilize low elevation

wetland habitats for multiple life history strategies and thus may be more sensitive to flooding of low-lying areas associated with heavy rainfall events (Woodrey et al., 2012). Specifically, while flooding in coastal marshes is usually discussed in the context of tidal fluctuations or extreme storm events, large rainfall events may increase projected groundwater-related flooding (Sukop et al., 2018) deepening foraging pools used by birds, which has been linked to decreases in habitat use by wading birds (Lantz et al., 2011), and reducing nesting success (Fletcher and Koford, 2004). Furthermore, marsh specialist species exhibit physiological adaptations to higher salinity environments compared to inland counterparts (Greenberg et al., 2006) suggesting potential competitive advantages in more saline environments. Reductions in salinity from increases in seasonal precipitation may alter these competitive advantages and facilitate increases in presence of more oligohaline bird species (Rush et al., 2009; Woodrey et al., 2012). In contrast, response of the total bird community to changes in dry season precipitation may be related to changes in food availability (e.g., increased insect abundance; Carroll et al., 2011; Robinson et al., 2007), altered disturbance regimes (e.g., increased fire frequency; Woodrey et al., 2012), and physiological stress (e.g., reduced water availability) experienced by resident, non-wetland bird species during the dry season (Illán et al., 2014). Thus, altered precipitation regimes under climate change appears to be another important driver of temporal avian biodiversity, with effects expected to strengthen in the future.

Temporal β-diversity for coastal bird communities was largely driven by changes in community turnover, as opposed to nestedness. This indicates that shifts in selective

ecological filters or sorting mechanisms (Legendre, 2014) caused by altered environmental and ecological conditions as discussed above were largely acting to changing the composition of avian communities without systematic loss or gain of species. Conversely, the higher proportion of total temporal β-diversity explained by nestedness in wetlands bird relative to all birds may have been driven by losses of sensitive species without replacement, consistent with trends for decreasing α-diversity for wetland birds. As wetland species should be especially sensitive to changes in wetland habitats, increasing mangrove encroachment and other land cover conversion may be having a disproportionate impact on these taxa.

Species richness was an important predictor of both relative change in α-diversity and temporal β-diversity across sites in the current study, which is consistent with findings of previous studies of biodiversity change in North American birds (Jarzyna and Jetz, 2017). The observed negative relationship between species richness and change in biodiversity may be partially driven by mechanisms related to the biotic resistance hypothesis, where sites with higher diversity preclude local colonizations derived from stronger biotic interaction strength compared to more depauperate sites (Freestone et al., 2013). Conversely, this relationship for both biodiversity metrics (relative change in α- and temporal β-diversity) may be an artifact of the metrics used. As both relative change in α-diversity and β_{Jac} are calculated based on changes in relative proportions of species within a community, gain or loss of a single species would have a smaller effect on total biodiversity change in species-rich communities (Koleff et al., 2003). Study duration was also an important predictor of total temporal β-diversity across sites, likely due to

increased capacity for change in systems over longer periods since both community shifts and changes in land cover and climate are often processes that occur over longer-time scales. While the positive relationship between temporal β-diversity and study duration is intuitive, it does highlight the value of using longer-duration time series to understand biodiversity change, especially if species experience delayed responses to changes in climate and land cover (Lemoine et al., 2007; La Sorte and Jetz, 2007).

I was able to explain up to 68% of variation in of biodiversity change across sites based on changes in climate and land cover, yet changes in bird biodiversity are likely governed by complex relationships beyond those investigated in this study. For example, while I focused on changes in cover of wetland and human-impacted land cover classes, other aspects of landscape configuration are known to impact avian species richness such as landscape heterogeneity and ecosystem diversity (Rahbek and Graves, 2001; Mohd-Azlan and Lawes, 2011). These metrics may be particularly useful for future models of α-diversity change as these models had poorer explanatory power in my analysis relative to those for temporal β-diversity. Similarly, while I considered land cover change within a 0.4-km buffer around routes based on BBS protocol (Sauer et al., 1997), it is likely that landscape changes at both finer and coarser scales were also important in mediating changes in avian community composition, although Veech et al. (2011) demonstrated that habitat types are relatively consistent at different scales around BBS routes. Moreover, in addition to the change in climatic means, anomalous climate events like floods or extreme heat events may act as important drivers of community composition (Van De Pol et al., 2010; Strong et al., 2015). While climatic means, minima, and maxima were all

highly correlated across sites in my analyses, changes in variation of climate variables or explicit climate extremes (i.e. number of extreme rainfall events) may help refine future models. Finally, sea-level rise has already been documented as a major threat to many coastal birds (Van De Pol et al., 2010; Field et al., 2018) and may drive patterns in coastal bird turnover that were unexplained in my analyses.

This study highlights the use of long-term, standardized monitoring datasets as a useful tool for detecting changes in ecological communities driven by environmental change at local to regional scales. Although the BBS dataset was limited to secondary roads and does not specifically target coastal locations, high spatial replication within the data set still allowed for the detection of changes in wetland bird community diversity. Combining such datasets with citizen science in the future may allow for increased spatial resolution or wider geographic extents to improve estimates of biodiversity change (Johnston et al., 2018). In the case of mangrove encroachment integrating bird observational datasets such as eBird (Sullivan et al., 2009) will provide spatial flexibility by individual observers if issues of observer bias and data quality can be overcome. Similarly, the North American Christmas Bird Count dataset (CBC; National Audubon Society) provides the opportunity to examine the impacts of mangrove encroachment on wintering birds of the GoM, many of which are in the order Charadriiformes, a group experiencing precipitous global declines (Kelleway et al., 2017; Rosenberg et al., 2019). However, the large spatial extent of individual CBC surveys may make restricting analyses to coastal ecosystems challenging as observers are not required to survey the entire extent of the survey area and may lead to underrepresented species and habitats.

Nonetheless, combining BBS data with citizen science or adding additional routes targeting coastal locations should help future efforts monitor biodiversity in dynamic coastal zones.

CONCLUSIONS

Coastal wetlands across the GoM represent extremely valuable habitat for avian communities, supporting highly diverse species assemblages and species of conservation concern. Human-induced changes to natural ecosystems are undeniably altering extant biodiversity in many ways, and this study provides critical evidence for large-scale changes in avian assemblages at regional scales. Based on trends in avian biodiversity over the last three decades, climate change appears to be impacting biodiversity of coastal avian communities via both changes in regional climate as well as range expansion of foundation species. In particular, the positive relationship between mangrove cover change and temporal β-diversity across sites suggests that areas near foundation species range boundaries may be hotspots of biodiversity change. These shifts in foundation species are likely to exacerbate changes in avian biodiversity driven by altered temperature and precipitation regimes under climate change. As climate and habitat models predict that the GoM coastal wetlands will continue to get hotter, wetter (Biasutti et al., 2012), and increasingly dominated by mangroves (Osland et al., 2013), documented shifts in avian biodiversity are only expected to strengthen. These findings highlight the need to incorporate information on range expansions of foundation species into models of climate change impacts on higher trophic level species. Furthermore, it

will be critical for land managers and policymakers to integrate results from studies such as this into current adaptive management and policy to effectively address climate-induced impacts on biodiversity in coastal wetlands across the Gulf of Mexico.

Table 1. Summary statistics and descriptions of the predictor variables used in mixed-effects and standard linear models for the diversity analyses. Δ denotes differences in accompanying predictor variable from start to end survey of each segment or route.

Environmental Variable (units)	***Scale***	***Description***	***Mean***	***SD***	***Range***
$\Delta T_{breeding}$ (°C)	Segment	Change in mean breeding season temperature (March – August)	0.43	0.36	-0.81 – 1.38
	Route		0.36	0.37	-0.55 – 1.14
ΔT_{Spring} (°C)	Segment	Change in mean spring temperature (April - June)	0.56	0.48	-0.91 – 1.76
	Route		0.48	0.48	-0.75 – 1.55
Δp_{wet} (cm)	Segment	Change in mean wet season precipitation (April – September)	1.88	2.30	-4.40 – 7.69
	Route		2.21	3.06	-3.63 – 15.47
Δp_{dry} (cm)	Segment	Change in mean dry season precipitation (October – March)	-0.16	2.05	-4.93 – 5.72
	Route		-0.13	2.52	-6.31 – 8.99
Δ Mangrove (%)	Segment	Change in percent cover mangrove (segment/route)	0.0012	0.021	-0.088 – 0.17
	Route		0.0009	0.014	-0.044 – 0.069

Table 1 (continued):

Δ Non-Mangrove Woody Wetland (%)	Segment	Change in percent cover woody wetland (segment/route)	0.065	0.17	-0.45 – 0.78
	Route		0.059	0.14	-0.26 – 0.68
Δ Emergent Wetland (%)	Segment	Change in percent cover emergent wetland (segment/route)	0.035	0.11	-0.30 – 0.51
	Route		0.034	0.08	-0.19 – 0.28
Δ Anthropogenic (%)	Segment	Change in percent cover anthropogenic (Agriculture/Urban) (segment/route)	0.019	0.14	-0.56 – 0.64
	Route		0.018	0.14	-0.556 – 0.49
Δ Upland Habitat (%)	Segment	Change in percent cover upland natural (Grassland/Forest) (segment/route)	-0.11	0.19	-0.92 – 0.19
	Route		-0.11	0.17	-0.81 – 0.16
Species Richness (# of spp.)	Segment	Site-specific species richness (# of spp.) at the last survey time	68.3	21	23 - 141
	Route		79	20.6	32 – 147
$SR_{Wetland}$ (# of spp.)	Segment	Site-specific wetland bird species richness (# of spp.) at the last survey time	22	11.9	4 - 61
	Route		26.6	13	7 - 61

Table 1 (continued):

Duration (Years)	Segment	Number of years between first and last survey date	23	11	4 – 37
	Route		23	11	4 – 37

Table 2. Summary statistics for diversity metrics used in analyses. Δ denotes differences in accompanying diversity metric from start to end survey of each segment or route. β-diversity indices are bound between 0 – 1 where 0 indicates zero dissimilarity and 1 is complete dissimilarity in community composition from start to end of each survey.

Metric	***Scale***	***Community***	***Mean***	***SD***	***Median***	***Range***
α-diversity (# spp.)	Segment	Total	68.3	21.10	70	23 – 141
	Route	Total	79	20.64	81	32 – 147
	Segment	Wetland	22	11.91	20	4 – 61
	Route	Wetland	26.6	12.99	25	7 – 61
Δ α-diversity (# spp.)	Segment	Total	-4.1	8.82	-3	-31 – 17
	Route	Total	-5	9.51	-4	-28 – 16
	Segment	Wetland	-2.5	4.65	-2	-20 – 8
	Route	Wetland	-2.9	5.08	-2	-20 – 10

Table 2 (continued):

%Δ α-diversity (Relative Change)	Segment	Total	-0.051	0.13	-0.05	-0.33 – 0.49
	Route	Total	-0.054	0.12	-0.04	-0.29 – 0.24
	Segment	Wetland	-0.079	0.23	-0.80	-0.67 – 1
	Route	Wetland	-0.078	0.21	-0.08	-0.5 – 0.86
β_{Jac}	Segment	Total	0.24	0.09	0.23	0.052 – 0.5
	Route	Total	0.22	0.09	0.22	0.03 – 0.42
	Segment	Wetland	0.31	0.18	0.29	0.02 – 0.76
	Route	Wetland	0.30	0.17	0.29	0.02 – 0.67
β_{Turn}	Segment	Total	0.16	0.09	0.15	0 – 0.43
	Route	Total	0.14	0.09	0.14	0.01 – 0.34
	Segment	Wetland	0.18	0.16	0.15	0 – 0.67
	Route	Wetland	0.18	0.16	0.17	0 – 0.58

Table 2 (continued):

β_{Nest}	Segment	Total	0.082	0.07	0.07	0 – 0.29
	Route	Total	0.079	0.07	0.05	0 – 0.25
	Segment	Wetland	0.13	0.11	0.10	0 – 0.67
	Route	Wetland	0.12	0.10	0.01	0 – 0.50
Slope β_{Jac}	Segment	Total	0.0044	0.0080	0.0037	-0.048 – 0.048
	Route	Total	0.0035	0.0081	0.0036	-0.042 – 0.040
	Segment	Wetland	0.0033	0.018	0.0035	-0.118 – 0.129
	Route	Wetland	0.0033	0.016	0.0037	-0.071 – 0.094

Table 2 (continued):

Slope α-diversity	Segment	Total	-0.089	1.095	-0.2	-8 – 7
	Route	Total	-0.097	0.695	-0.194	-1.35 – 2.7
	Segment	Wetland	-0.168	0.960	-0.086	-9 – 5
	Route	Wetland	-0.115	0.418	-0.096	-2 – 1.87
ΔCMRL (°)	Route	Total	-0.37	0.72	-0.26	-2.7 – 0.86

Table 3. Summary of segment-level linear mixed-effects model output of relative change in α-diversity for both total (shaded region) and wetland bird (non-shaded region) community composition**.** Bold rows indicate significant effects of predictors ($p < 0.05$). Random effects components and model fit presented below. Rows with missing values correspond to predictors that were not used for the corresponding response variables.

	Relative Change α-diversity			*Relative Change Wetland Bird α-diversity*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	**-0.18**	**-0.28 – -0.08**	**<0.001**	-0.07	-0.20 – 0.07	0.334
Δ p_{wet} (cm)	-0.01	-0.02 – 0.00	0.203	-0.00	-0.02 – 0.01	0.691
Δ p_{dry} (cm)	-0.01	-0.02 – 0.01	0.333	-0.01	-0.03 – 0.01	0.601
Δ $T_{breeding}$ (°C)	-0.01	-0.08 – 0.06	0.748	-0.01	-0.14 – 0.12	0.860
Δ Mangrove Cover (%)	**-0.01**	**-0.01 – -0.00**	**0.020**	**-0.02**	**-0.03 – -0.00**	**0.017**
Δ Emergent Wetland Cover (%)	0.00	-0.00 – 0.00	0.105	0.00	-0.00 – 0.00	0.248
Δ Non-Mangrove Woody Wetland Cover (%)	0.00	-0.00 – 0.00	0.713	-0.00	-0.00 – 0.00	0.775
Δ Anthropogenic Cover (%)	0.00	-0.00 – 0.00	0.304	0.00	-0.00 – 0.00	0.220
Duration of Survey (Years)	-0.00	-0.01 – 0.00	0.057	-0.00	-0.01 – 0.00	0.105

Table 3 (continued):

Species Richness	**0.00**	**0.00 – 0.00**	**<0.001**			
Wetland Bird Species Richness				**0.00**	**0.00 – 0.01**	**0.020**
Random Effects						
σ^2		0.00			0.03	
τ_{00}		0.01 $_{\text{Route}}$			0.02 $_{\text{Route}}$	
ICC		0.73			0.45	
N		73 $_{\text{Route}}$			73 $_{\text{Route}}$	
Observations		241			241	
Marginal R^2 / Conditional R^2		**0.274** / 0.806			**0.109** / 0.513	

Table 4. Summary of route-level multiple regression model output of relative change in α-diversity for both total (shaded region) and wetland bird (non-shaded region) community composition**.** Bold rows indicate significant effects of predictors ($p < 0.05$). Rows with missing values correspond to predictors that were not used for the corresponding response variables.

	Relative Change α-diversity			*Relative Change Wetland Bird α-diversity*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	-0.10	-0.22 – 0.03	0.131	-0.04	-0.22 – 0.14	0.655
Δ p_{wet} (cm)	0.00	-0.01 – 0.01	0.597	0.00	-0.01 – 0.02	0.704
Δ p_{dry} (cm)	0.00	-0.01 – 0.01	0.910	-0.00	-0.02 – 0.02	0.755
Δ $T_{breeding}$ (°C)	-0.05	-0.13 – 0.03	0.195	-0.06	-0.21 – 0.09	0.420
Δ Mangrove Cover (%)	-0.02	-0.04 – 0.00	0.062	-0.03	-0.07 – 0.00	0.087
Δ Emergent Wetland Cover (%)	-0.00	-0.00 – 0.00	0.959	0.00	-0.01 – 0.01	0.682
Δ Non-Mangrove Woody Wetland Cover (%)	-0.00	-0.00 – 0.00	0.601	-0.00	-0.01 – 0.00	0.747
Δ Anthropogenic Cover (%)	0.00	-0.00 – 0.00	0.388	0.00	-0.00 – 0.01	0.330
Duration of Survey (Years)	-0.00	-0.00 – 0.00	0.215	-0.00	-0.01 – 0.00	0.225

Table 4 (continued):

Species Richness	**0.00**	**0.00 – 0.00**	**0.049**			
Wetland Bird Species Richness				0.00	-0.00 – 0.01	0.295
Observations		73			73	
R^2		**0.194**			**0.118**	

Table 5. Summary of segment-level generalized linear mixed-effects model output of β-diversity for both total (shaded region) and wetland bird (non-shaded region) community composition**.** Parameter estimates are untransformed and represented on the logit scale. Bold rows indicate significant effects of predictors ($p < 0.05$). Random effects components and model fit presented below. Rows with missing values correspond to predictors that were not used for the corresponding response variables.

	Total Bird Community β-diversity (β_{Jac})			*Wetland Bird β-diversity (β_{Jac})*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	**-0.79**	**-1.12 – -0.46**	**<0.001**	-0.24	-0.64 – 0.15	0.221
Δ p_{wet} (cm)	**0.03**	**0.00 – 0.06**	**0.036**	**0.05**	**0.00 – 0.10**	**0.048**
Δ p_{dry} (cm)	-0.01	-0.05 – 0.03	0.556	-0.00	-0.06 – 0.05	0.881
Δ $T_{breeding}$ (°C)	-0.06	-0.28 – 0.16	0.578	0.00	-0.36 – 0.36	0.998
Δ Mangrove Cover (%)	**0.03**	**0.01 – 0.04**	**<0.001**	**0.05**	**0.03 – 0.08**	**<0.001**
Δ Emergent Wetland Cover (%)	0.00	-0.00 – 0.00	0.601	-0.00	-0.01 – 0.00	0.622
Δ Non-Mangrove Woody Wetland Cover (%)	0.00	-0.00 – 0.00	0.680	-0.00	-0.01 – 0.00	0.297
Δ Anthropogenic Cover (%)	-0.00	-0.00 – 0.00	0.880	-0.00	-0.01 – 0.00	0.158

Table 5 (continued):

Duration of Survey (Years)	**0.02**	**0.01 – 0.02**	**0.001**	**0.01**	**0.00 – 0.03**	**0.031**
Species Richness	**-0.01**	**-0.02 – -0.01**	**<0.001**			
Wetland Bird Species Richness				**-0.05**	**-0.06 – -0.04**	**<0.001**
Random Effects						
σ^2		0.04			0.14	
τ_{00}		0.11_{Route}			0.23_{Route}	
ICC		0.74			0.62	
N		73_{Route}			73_{Route}	
Observations		241			241	
Marginal R^2 / Conditional R^2		**0.451** / 0.857			**0.543** / 0.827	

Table 6. Summary of generalized linear model output of β-diversity for both total (shaded region) and wetland bird (non-shaded region) community composition**.** Bold rows indicate significant effects of predictors ($p < 0.05$). Phi is an estimate of model precision. Rows with missing values correspond to predictors that were not used for the corresponding response variables.

	Total Bird Community β-diversity (β_{Jac})			*Wetland Bird β-diversity (β_{Jac})*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	**-0.58**	**-0.93 – -0.23**	**0.001**	-0.01	-0.43 – 0.42	0.973
Δ p_{wet} (cm)	0.02	-0.00 – 0.05	0.067	**0.05**	**0.01 – 0.09**	**0.021**
Δ p_{dry} (cm)	**0.04**	**0.01 – 0.07**	**0.014**	0.04	-0.01 – 0.09	0.123
Δ $T_{breeding}$ (°C)	**0.48**	**0.26 – 0.71**	**<0.001**	**0.63**	**0.28 – 0.97**	**<0.001**
Δ Mangrove Cover (%)	0.04	-0.01 – 0.09	0.104	0.06	-0.02 – 0.14	0.160
Δ Emergent Wetland Cover (%)	-0.01	-0.02 – 0.00	0.262	-0.01	-0.02 – 0.01	0.258
Δ Non-Mangrove Woody Wetland Cover (%)	**0.01**	**0.00 – 0.01**	**0.026**	0.00	-0.01 – 0.01	0.558
Δ Anthropogenic Cover (%)	-0.00	-0.01 – 0.00	0.553	**-0.01**	**-0.02 – -0.00**	**0.034**
Duration of Survey (Years)	**0.01**	**0.00 – 0.02**	**0.015**	0.01	-0.01 – 0.02	0.280

Table 6 (continued):

Species Richness	**-0.02**	**-0.02 – -0.01**	**<0.001**			
Wetland Species Richness				**-0.05**	**-0.06 – -0.04**	**<0.001**
Phi (ϕ)	**4.06**	**3.74 – 4.38**	**<0.001**	**2.97**	**2.65 – 3.29**	**<0.001**
Observations		73			73	
Pseudo R^2		**0.649**			**0.688**	

Table 7. Summary of linear model output of total bird community β-diversity (shaded region), total bird community turnover (non-shaded region), total bird community nestedness (shaded region), and Δ CMRL (non-shaded region) community composition**.** Bold rows indicate significant effects of predictors ($p < 0.05$). Rows with missing values correspond to predictors that were not used for the corresponding response variables.

	Total Bird Community β-diversity (β_{Jac})			*Total Bird Community Turnover (β_{Turn})*			*Total Bird Community Nestedness (β_{Nest})*			*Change in CMRL (°)*		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
Intercept	**0.21**	**0.18 – 0.23**	**<0.001**	**0.13**	**0.11 – 0.15**	**<0.001**	**0.08**	**0.06 – 0.09**	**<0.001**	-8.30	-0.29 – 0.14	0.50
Δ CMRL (°)	**-0.04**	**-0.07 – -0.01**	**0.01**	**-0.03**	**-0.06 – -0.00**	**0.02**	-0.01	-0.03 – 0.01	0.47			
Δ T_{Spring} (° C)										**-0.61**	**-0.93 – -0.29**	**<0.001**
Observations	73			73			73			73		
R^2 / R^2 adjusted	**0.11** / 0.09			**0.07** / 0.06			**0.01** / -0.01			**0.17** / 0.16		

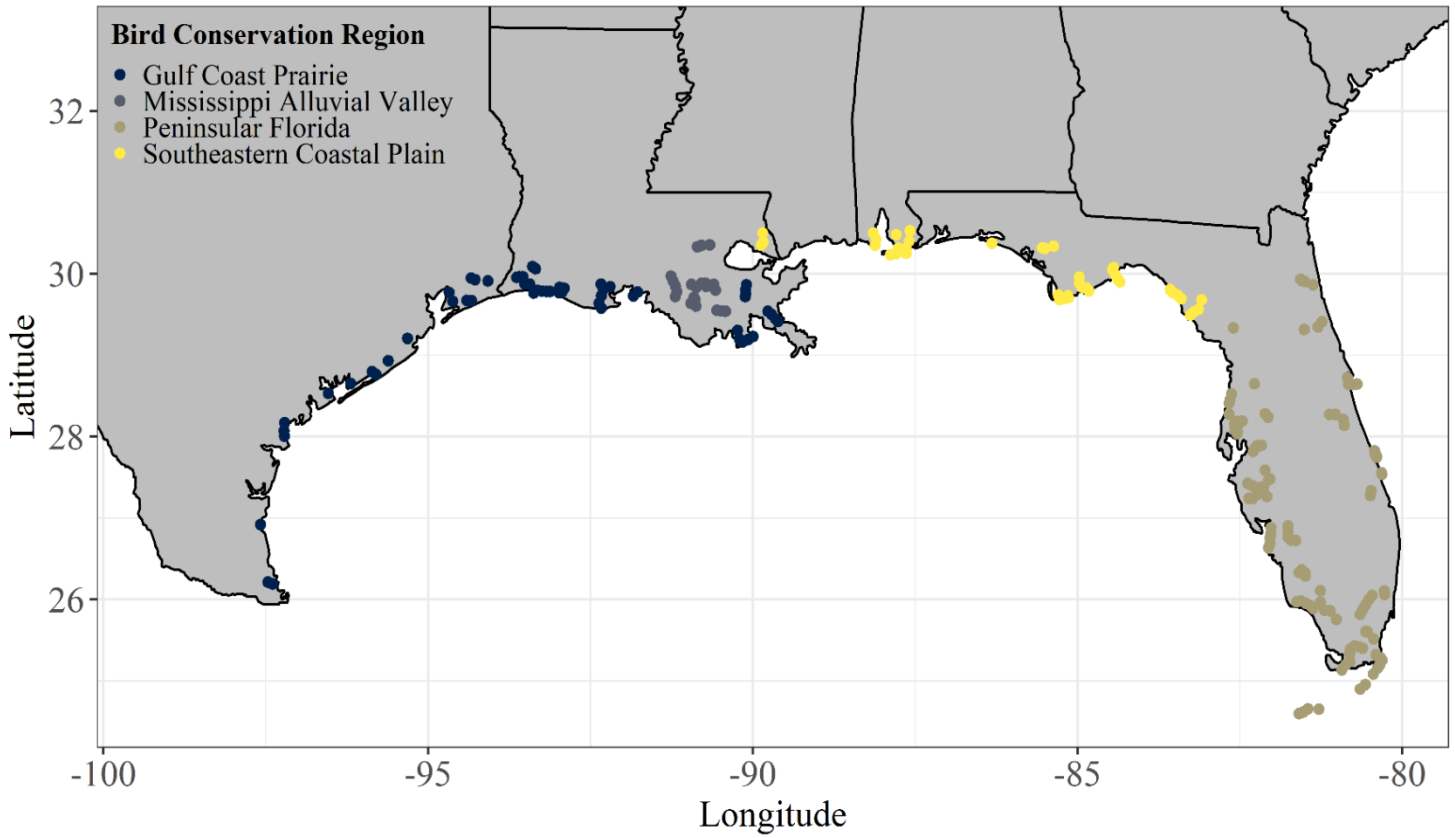

Figure 1. Map of sites used in this study. Individual points represent Breeding Bird Survey segments used for biodiversity analyses. Site color corresponds to associated Bird Conservation Region (BCR).

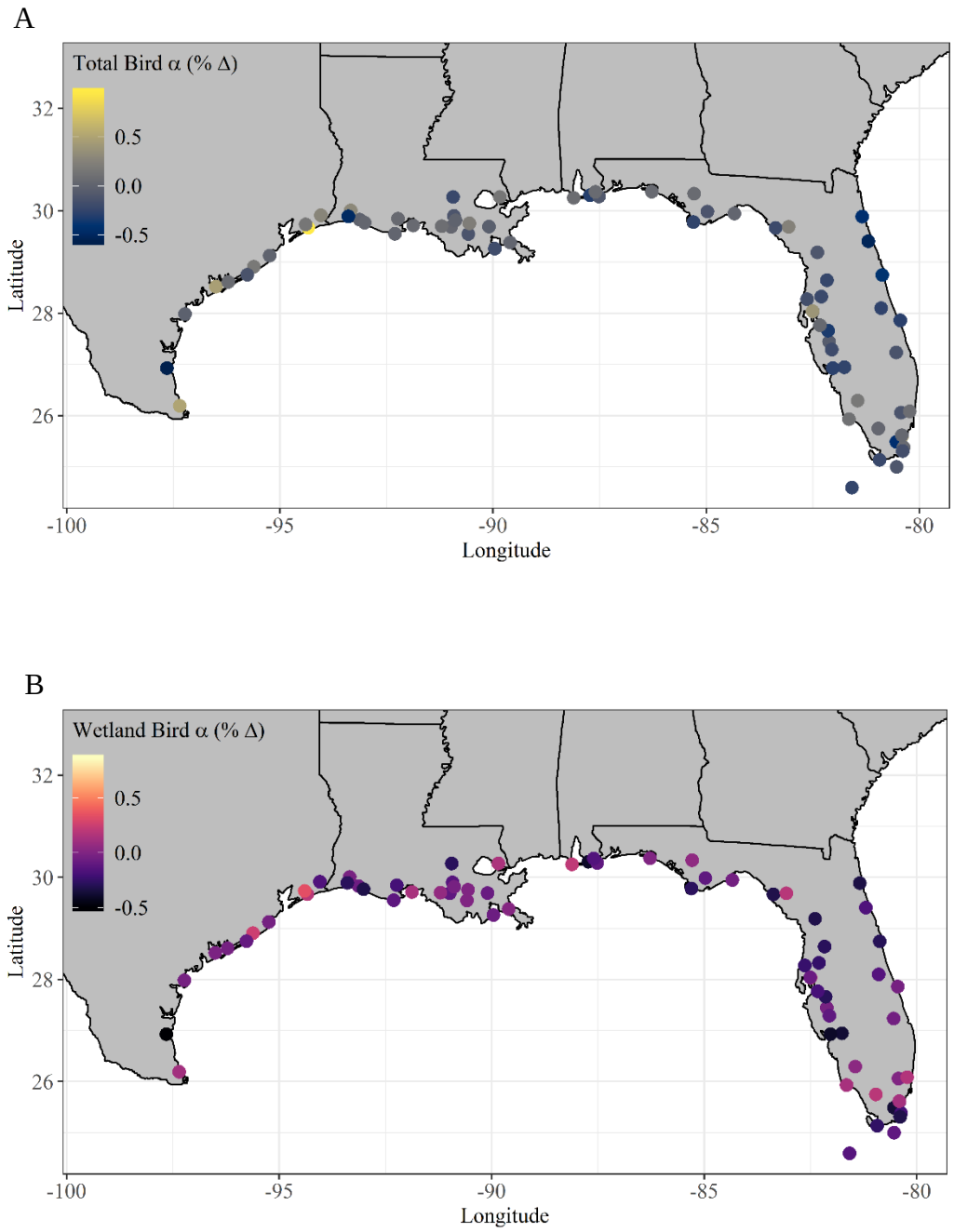

Figure 2. Map of relative change in α-diversity (%Δα) for (A) the total bird community and (B) wetland bird community. Lighter colors indicate positive change and darker colors indicate negative change in both maps. Points correspond to route-level changes in α-diversity taken from survey end points.

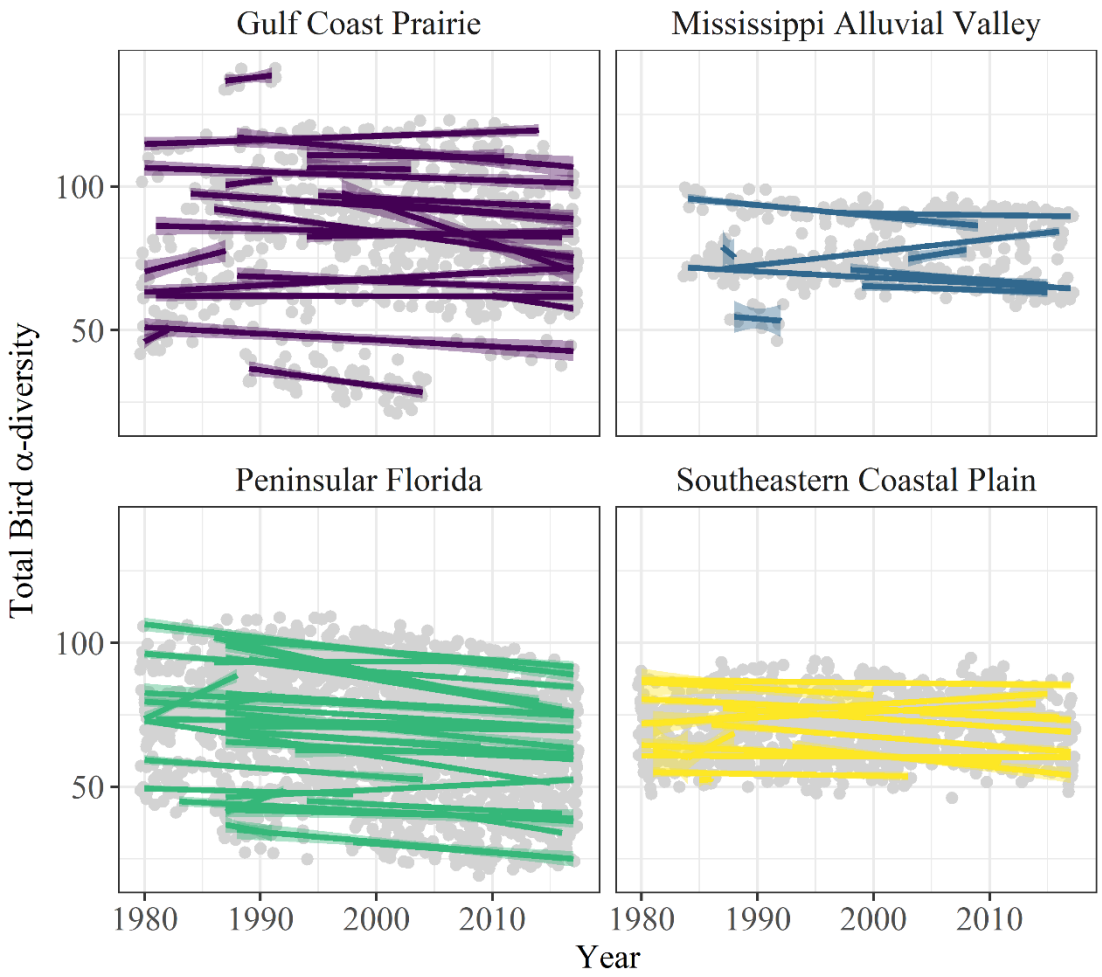

Figure 3. Patterns of detection-corrected, route-level total bird α-diversity (# of species) across the entire time series by Bird Conservation Region. Individual lines represent a single route within each BCR (differentiated by color).

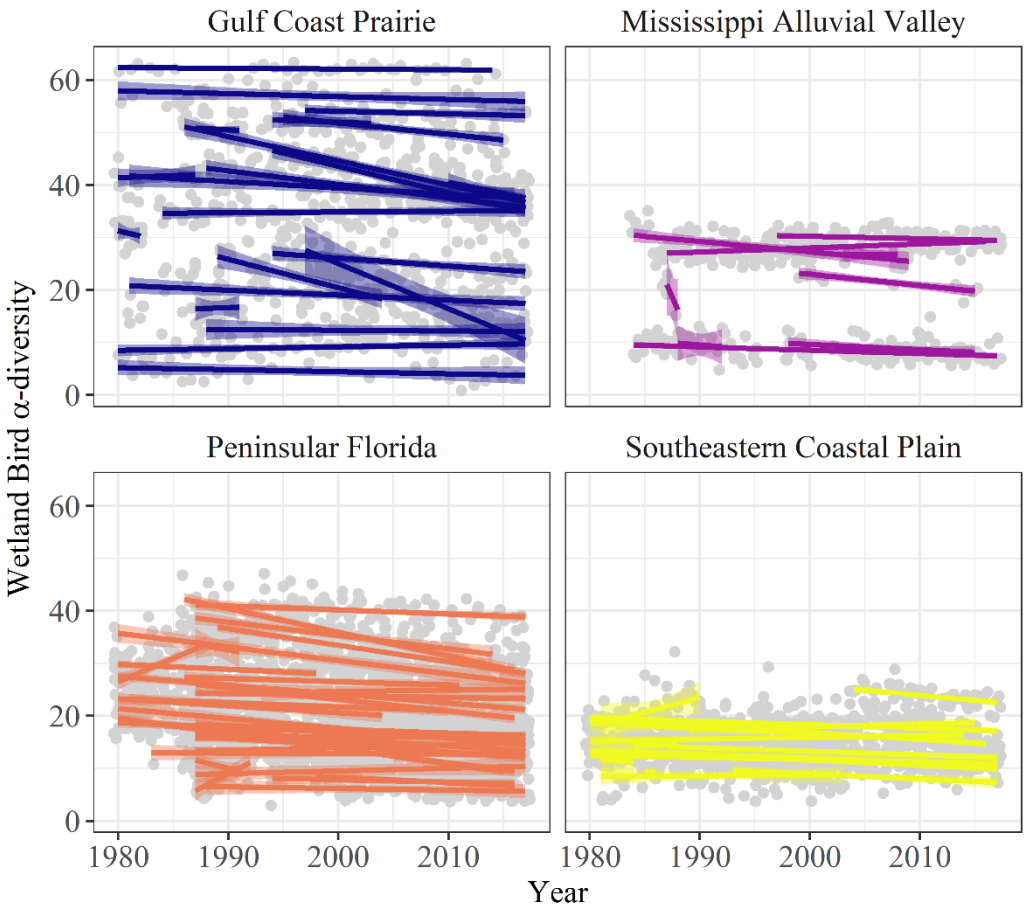

Figure 4. Patterns of detection-corrected, route-level wetland bird α-diversity (# of species) across the entire time series by Bird Conservation Region. Individual lines represent a single route within each BCR (differentiated by color).

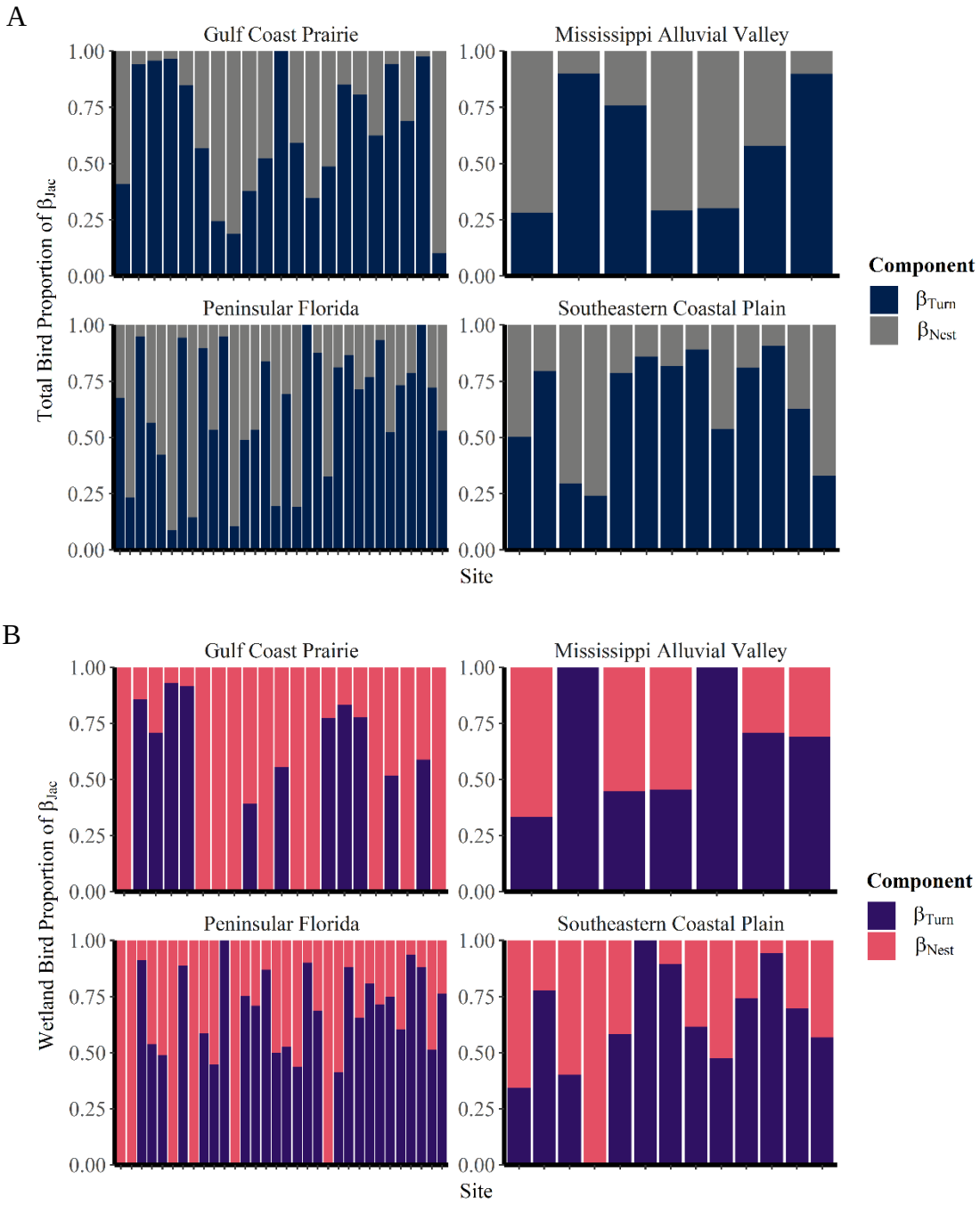

Figure 5. Relative contribution of turnover (β_{Turn}) and nestedness (β_{Nest}) for each site used in this study. Plots are representative of proportions of contribution between each component out of total beta diversity (β_{Jac}).

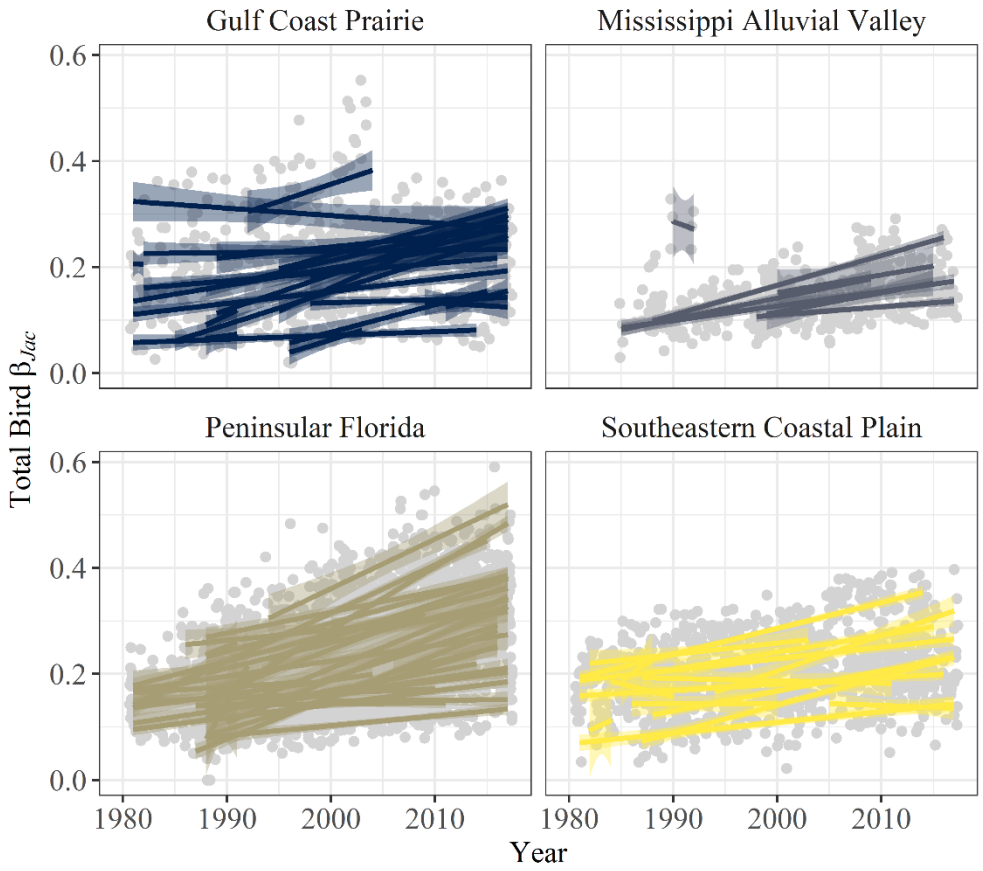

Figure 6. Patterns of detection-corrected, route-level total bird community temporal β-diversity (β_{Jac}) across the entire time series separated by Bird Conservation Region. β-diversity represents Jaccard dissimilarity ranging from 0 – 1, where 0 indicates no temporal dissimilarity and 1 indicated complete community dissimilarity.

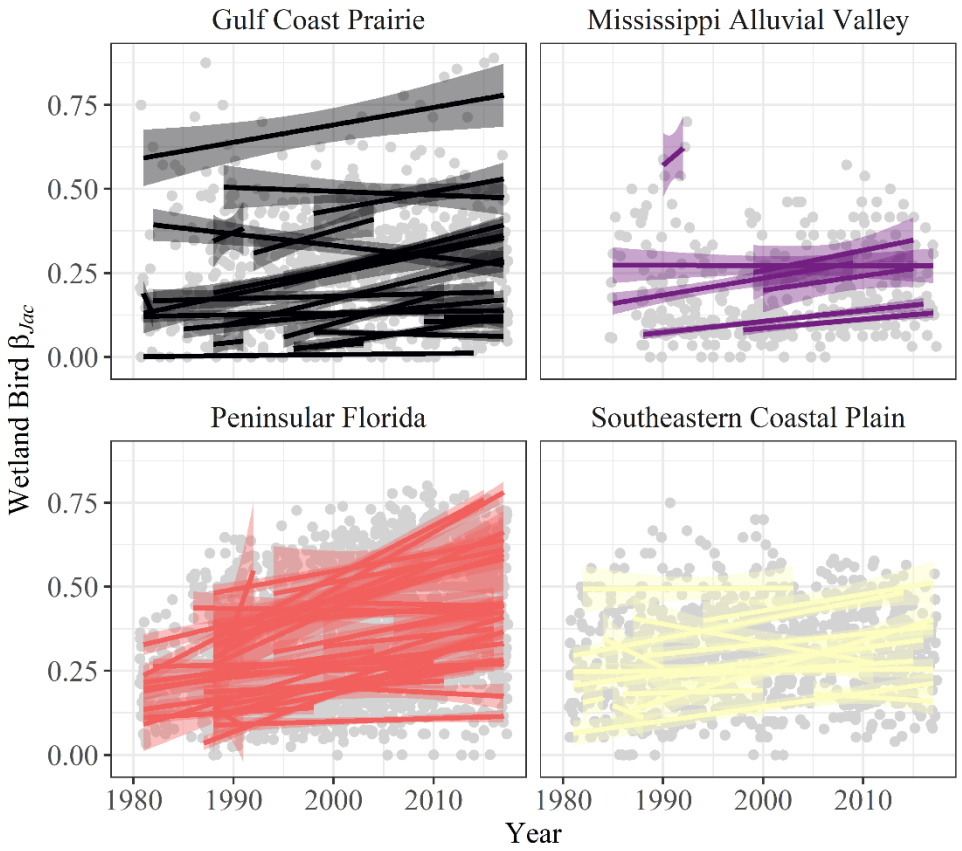

Figure 7. Patterns of detection-corrected, route-level wetland bird community temporal β-diversity (β_{Jac}) across the entire time series separated by Bird Conservation Region. β-diversity represents Jaccard dissimilarity ranging from 0 – 1, where 0 indicates no temporal dissimilarity and 1 indicated complete community dissimilarity.

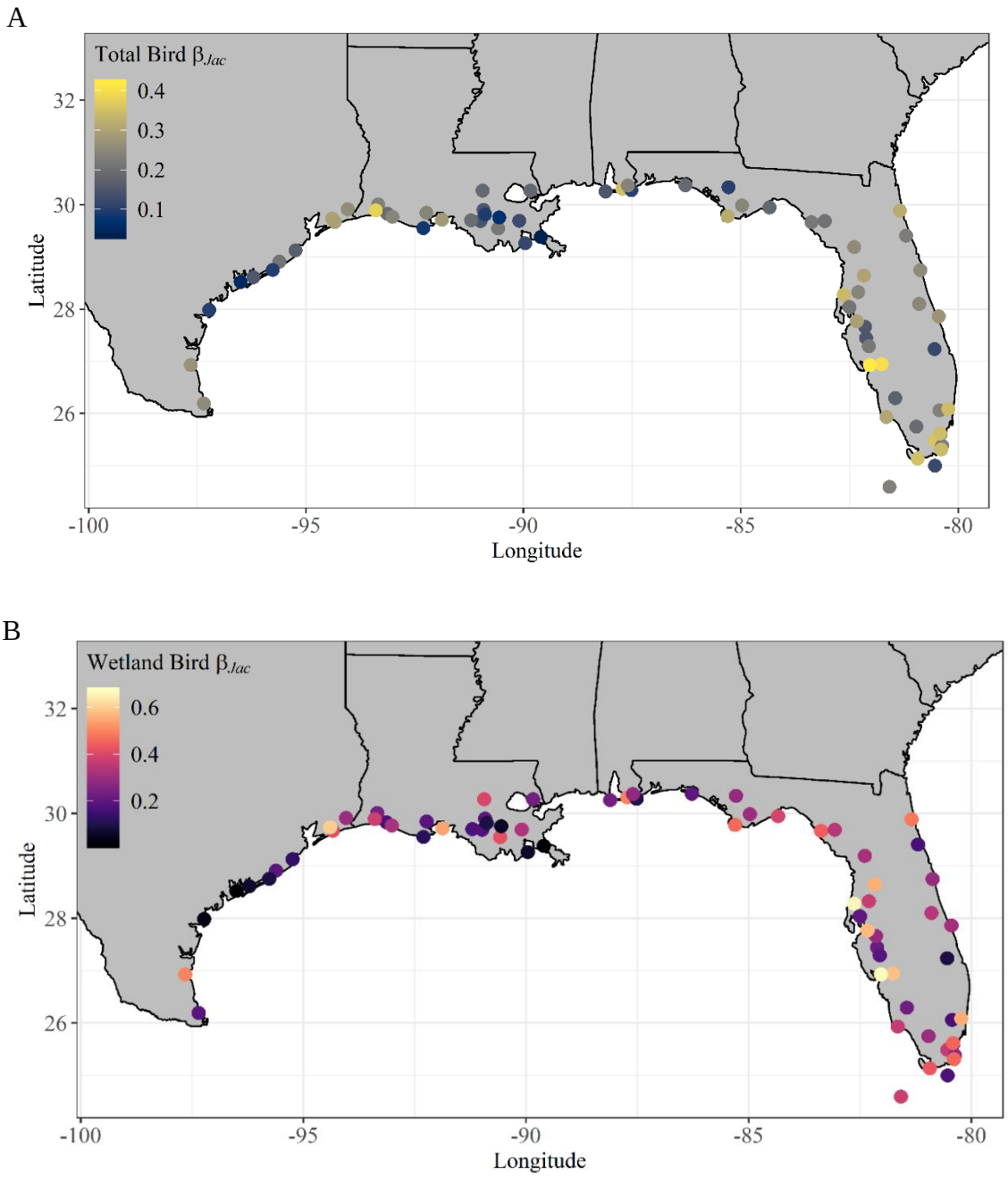

Figure 8. Map of total β-diversity (β_{Jac}) for (A) total bird community dissimilarity and (B) wetland bird community dissimilarity. Lighter colors indicate higher levels of community turnover in both maps. Points correspond to route-level changes in beta diversity taken from survey end points.

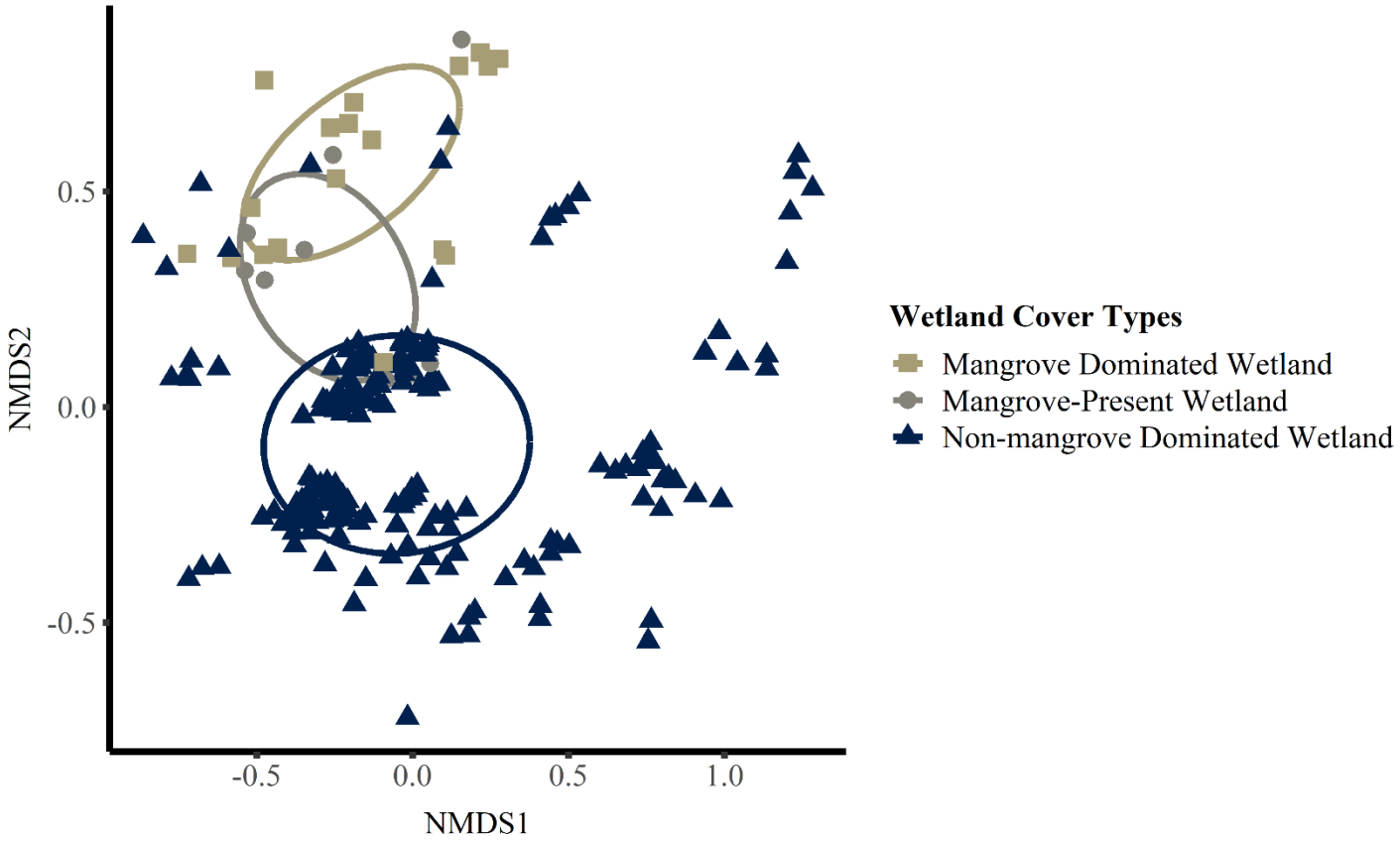

Figure 9. NMDS plots of Jaccard dissimilarity between sites from pooled avian communities between 1980 – 1989 and 1990 – 2000 for three wetland classes related to mangrove cover (mangrove dominated, mangrove-present, and non-mangrove dominated). Colors and shapes correspond to the respective habitat classification described in the methods.

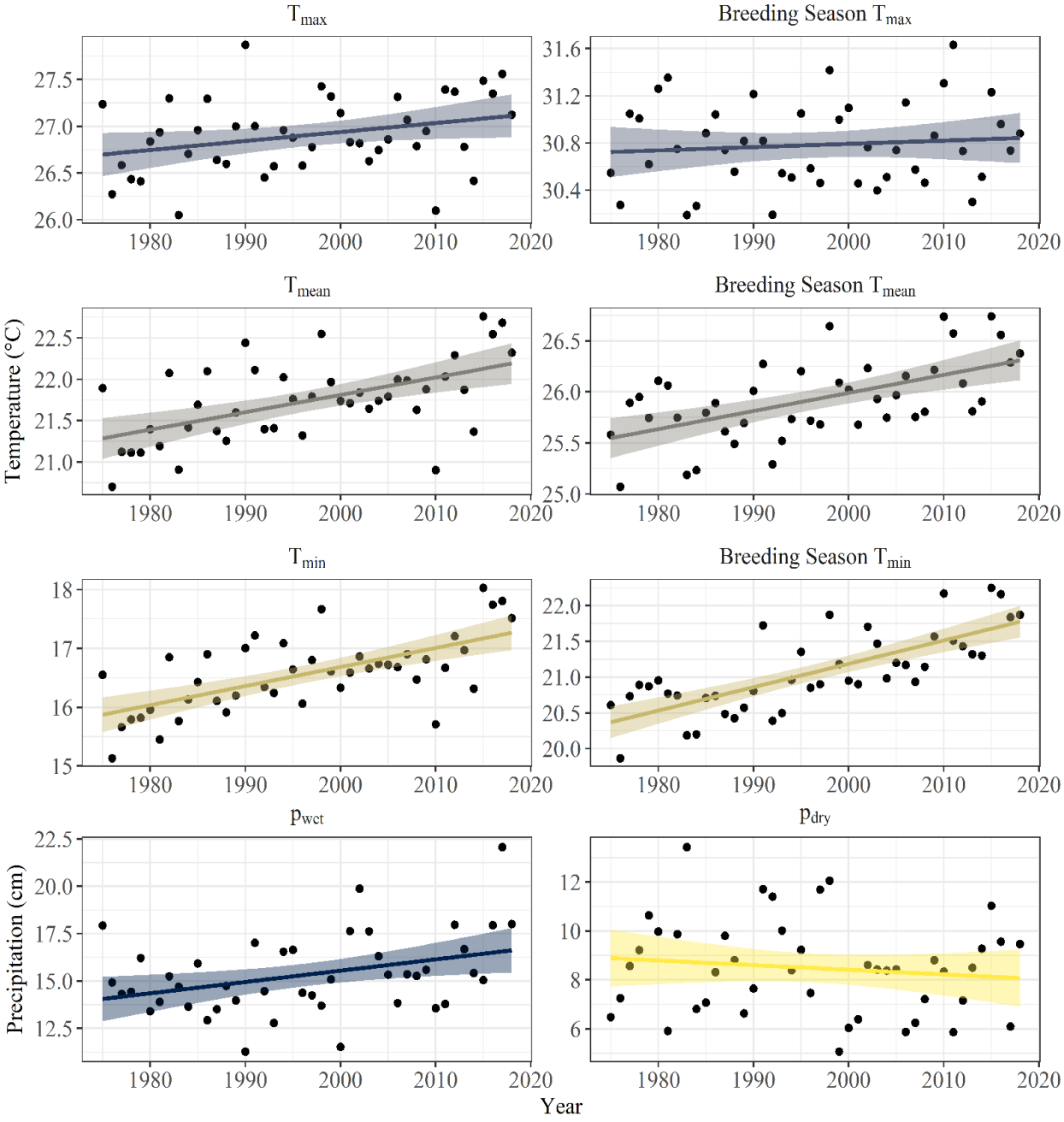

Figure 10. Temporal trends of relevant climate variables from 1975 – 2017 for mean annual temperature covariates, mean breeding season temperature covariates (March – August), mean dry season precipitation (November – April), and mean wet season precipitation (May – September).

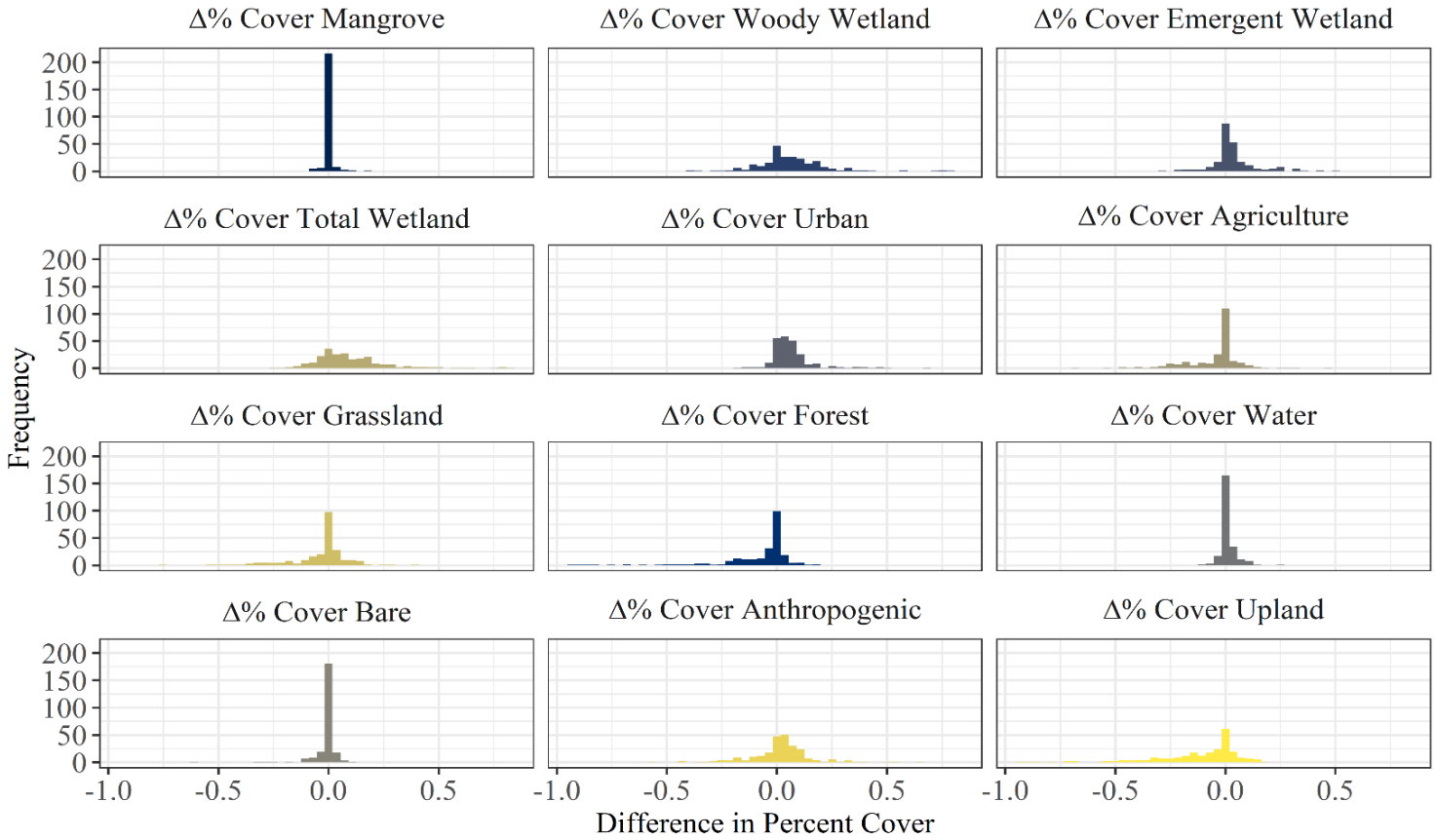

Figure 11. Histograms of changes in land cover (% cover) classes for sites used in analyses. Changes were calculated from start to end of each respective survey site. Percent change in Anthropogenic land cover is a summation of urban and agricultural land cover classes. Percent change in Upland land cover is a summation of grassland and forest land cover classes.

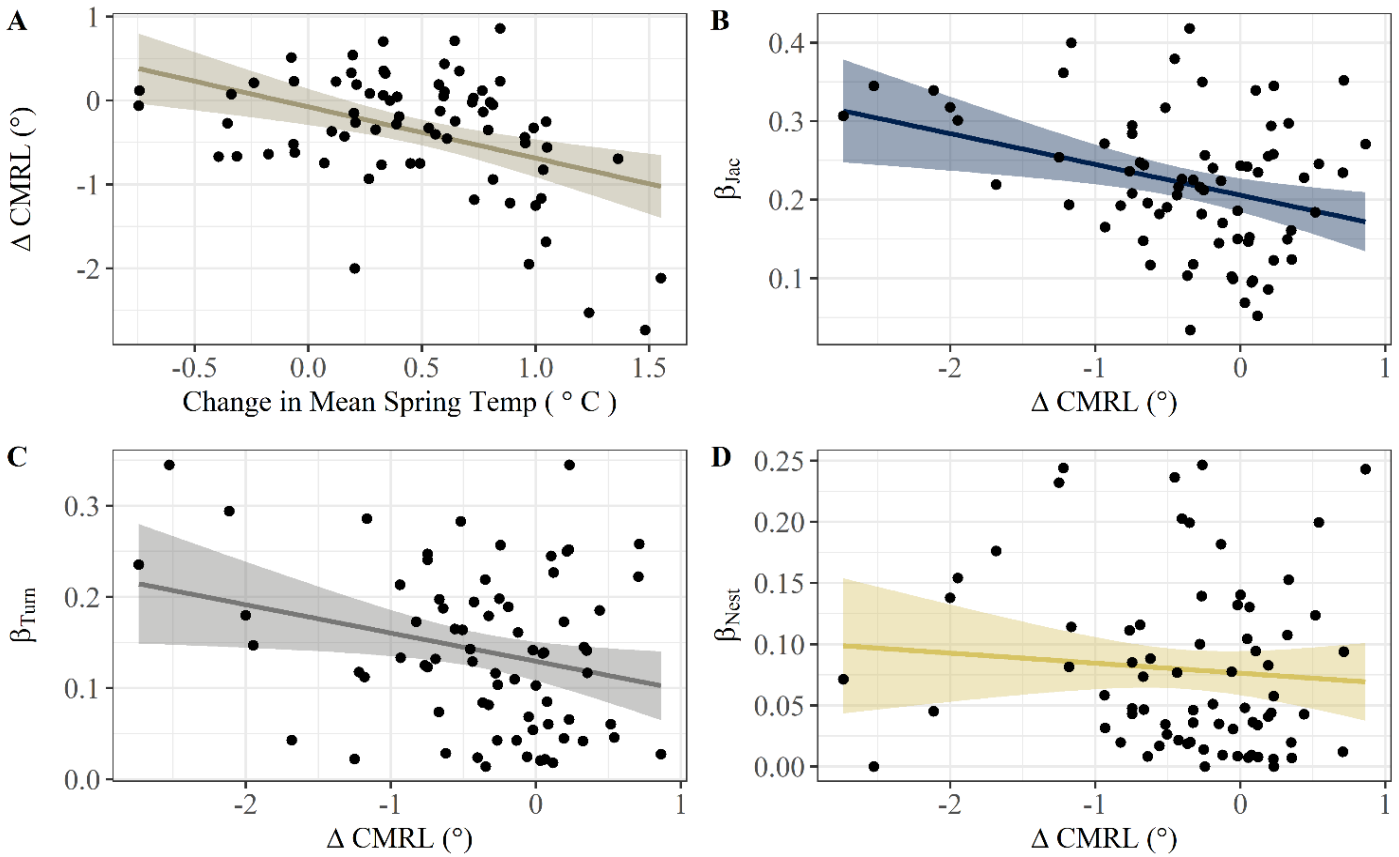

Figure 12. (A) Relationship between change in mean spring temperature, (B) total beta diversity (β_{Jac}) relative to changes in CMRL, (C) turnover component of beta diversity (β_{Turn}) relative to changes in CMRL, and (D) nestedness component of beta diversity (β_{Nest}) relative to changes in CMRL. Beta diversity and CMRL corresponds to final survey point.

Appendix

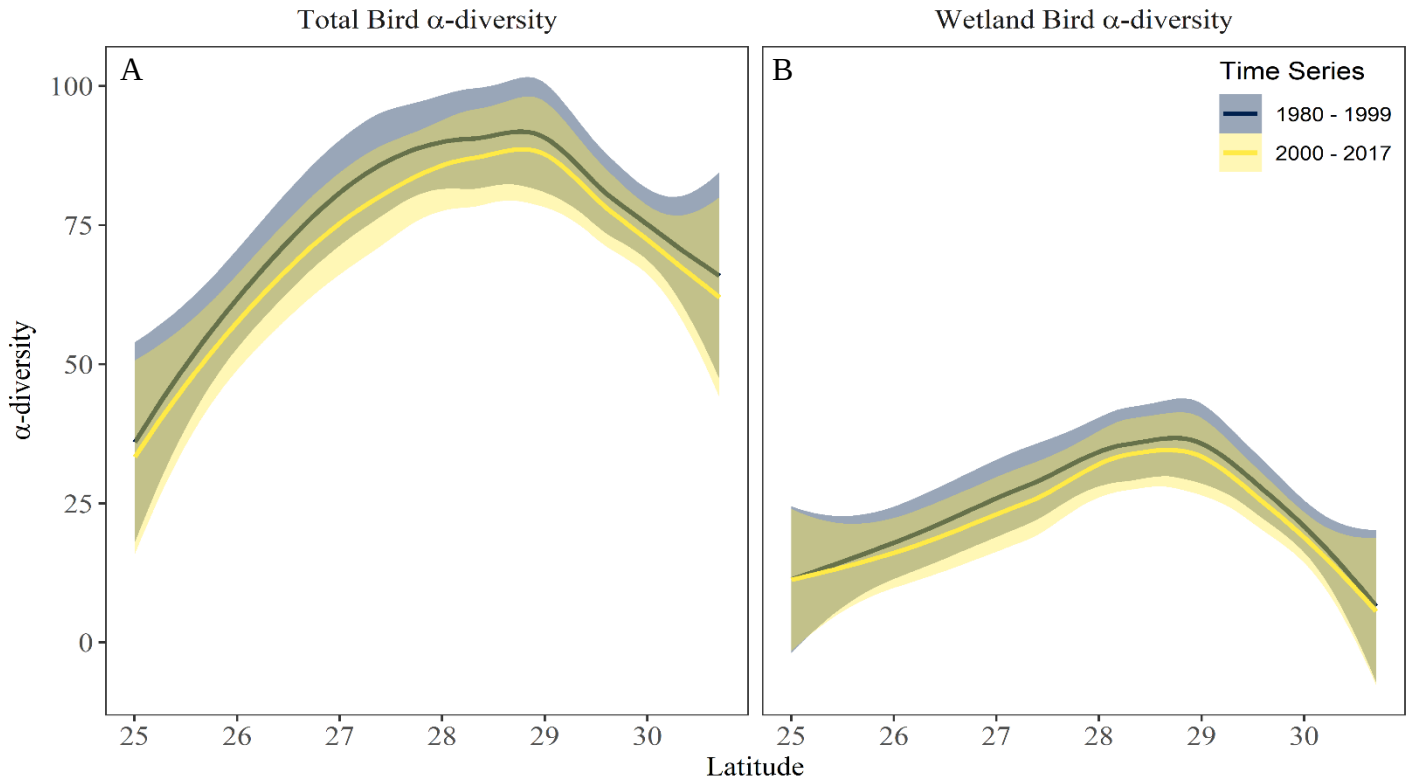

Figure 13. Plots showing latitudinal relationship between average (A) total bird community α-diversity and (B) wetland bird community α-diversity between two time periods: 1980 – 1999 and 2000 – 2017.

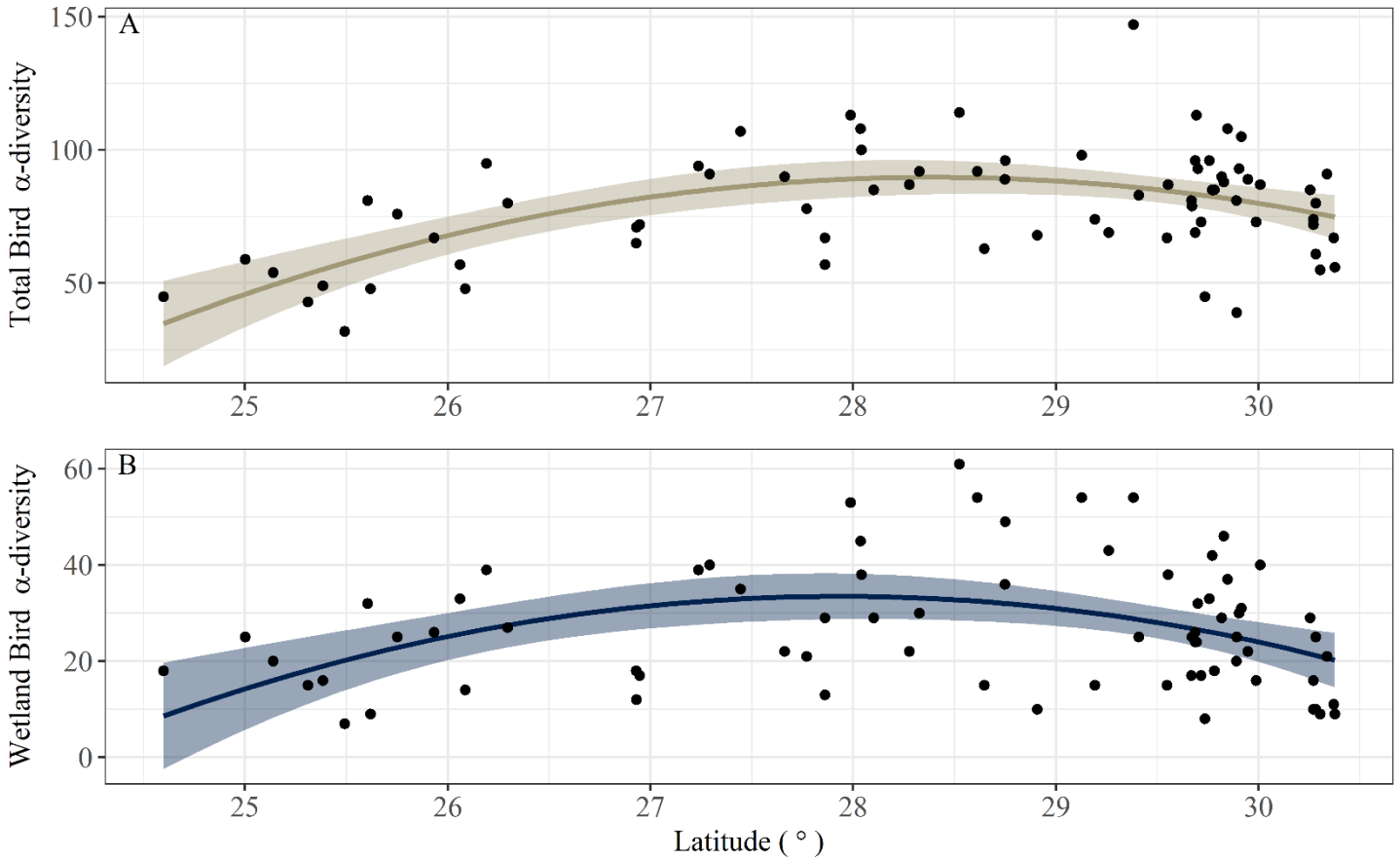

Figure 14. Detection-corrected bird α-diversity relative to latitude for (A) total bird communities and (B) wetland-associated bird communities. Shading represents 95% credible intervals for predicted relationship between species richness and latitude. Linear relationships expressed as quadratic relationship with diversity peaking for both communities at ~28° N. Species richness corresponds to final survey point for each site.

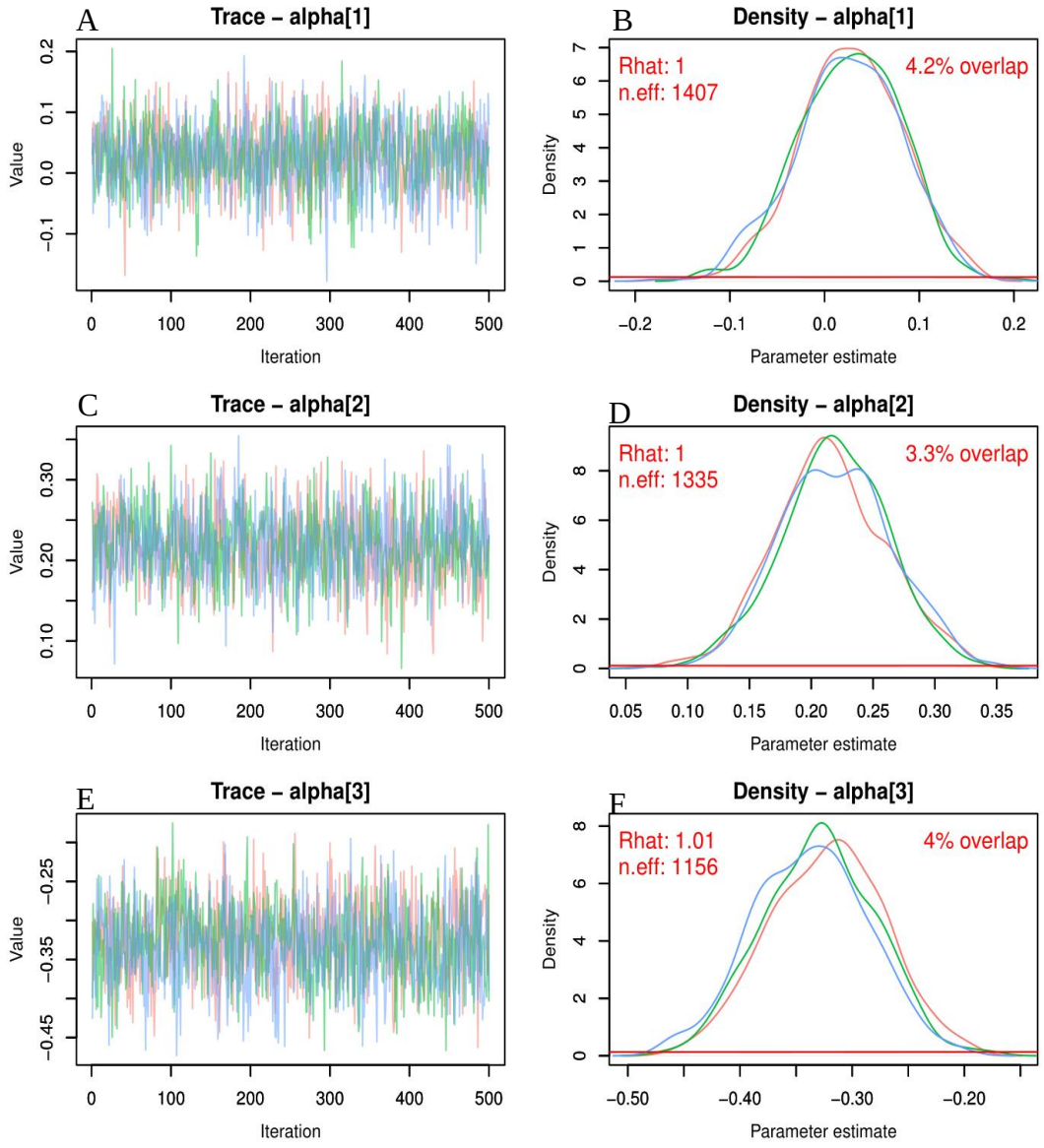

Figure 15. Example of Markov Chain Monte Carlo output for predictor variables in detection sub-model for multispecies occupancy model. Plots A, C, and E represent convergence of 3 chains (red, green, and blue) on parameter estimates over 500 iterations. Plots B, D, and F represent density plots of distributions for estimated parameters for each chain (red, green, blue). Overlap corresponds to the posterior distributional estimate overlap with prior distribution (dark red) for each parameter. Gelman-Rubin convegence diagnostic presented within plot at "Rhat", Rhat < 1.1 indicate sufficient parameter convergence.

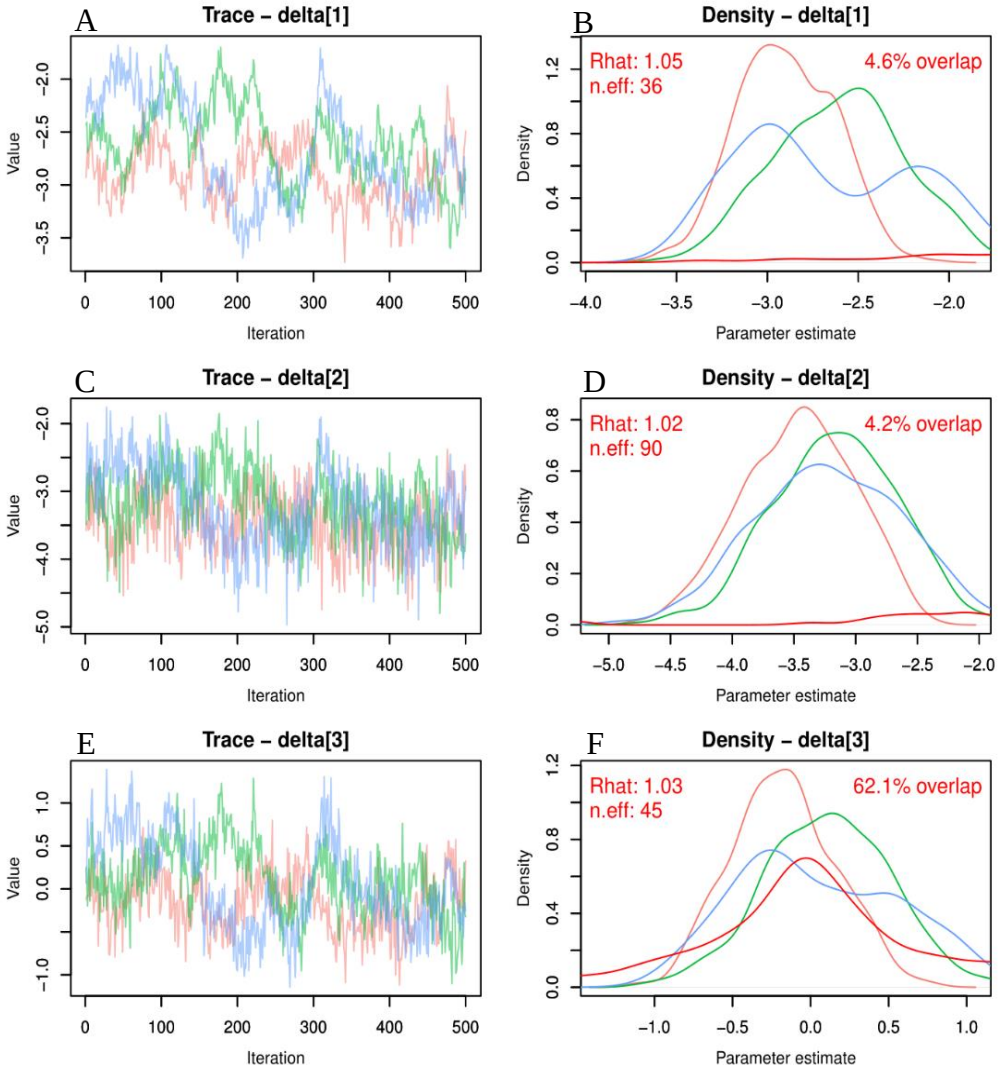

Figure 16. Example of Markov Chain Monte Carlo output for random effects of species variables in detection sub-model for multispecies occupancy model. Plots A, C, E inidcate convergence of 3 chains (red, green, and blue) on parameter estimates over 500 iterations. Plots B, D, F indicate density plots of distributions for estimated parameters for each chain (red, green, blue). Overlap corresponds to the posterior distributional estimate overlap with prior distribution (dark red) for each parameter. Gelman-Rubin convegence diagnostic presented within plot at "Rhat", Rhat < 1.1 indicate sufficient parameter convergence.

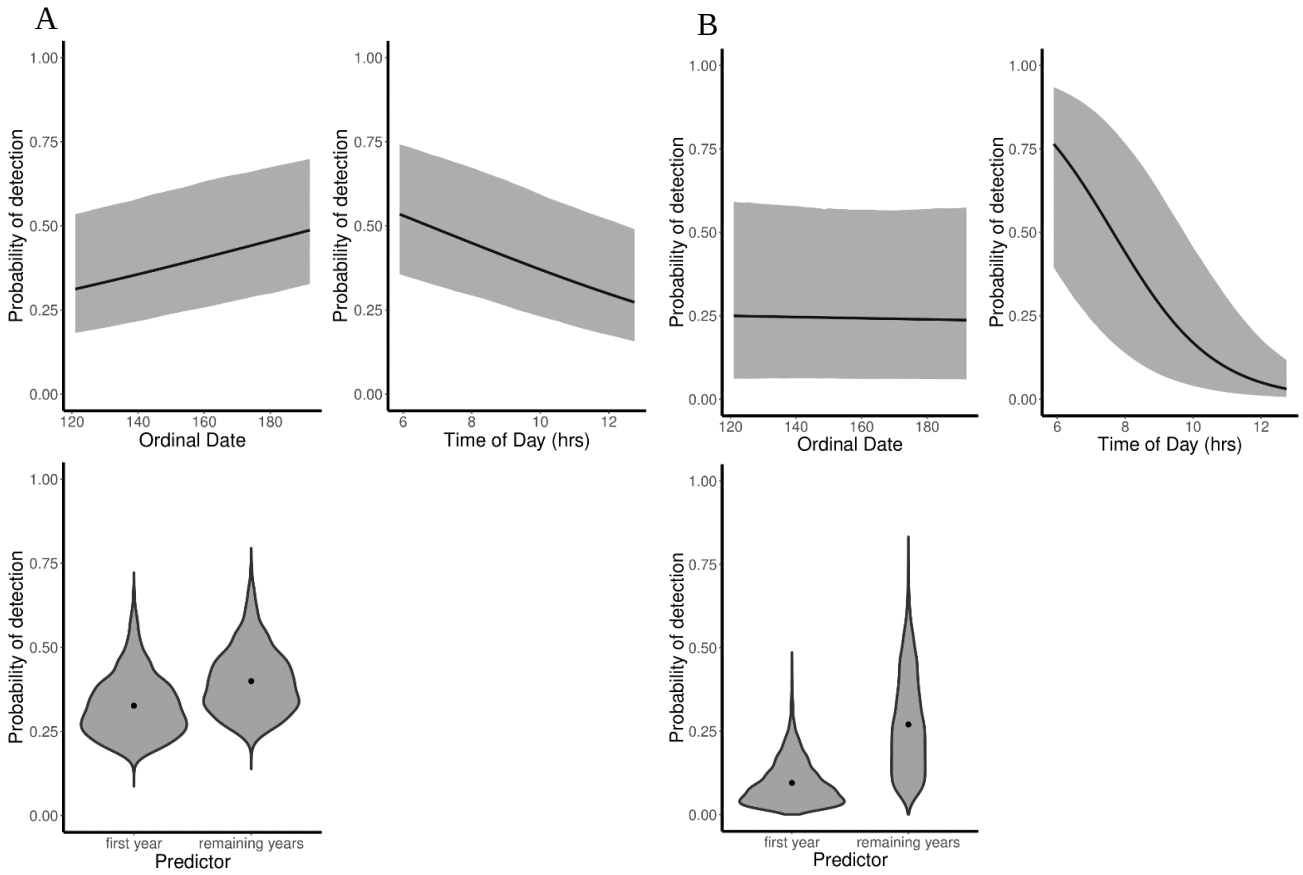

Figure 17. Example of predictor relationships with species detection probability in the detection sub-model of the multispecies occupancy model for phylogenetic groups (A) Podicipediformes/Gruiformes *(Grebes/Rails)* and (B) Strigiformes *(Owls)*. Plots demonstrate the relationhsips between detection probability and ordinal date, time of day (hrs), and first-year observers.

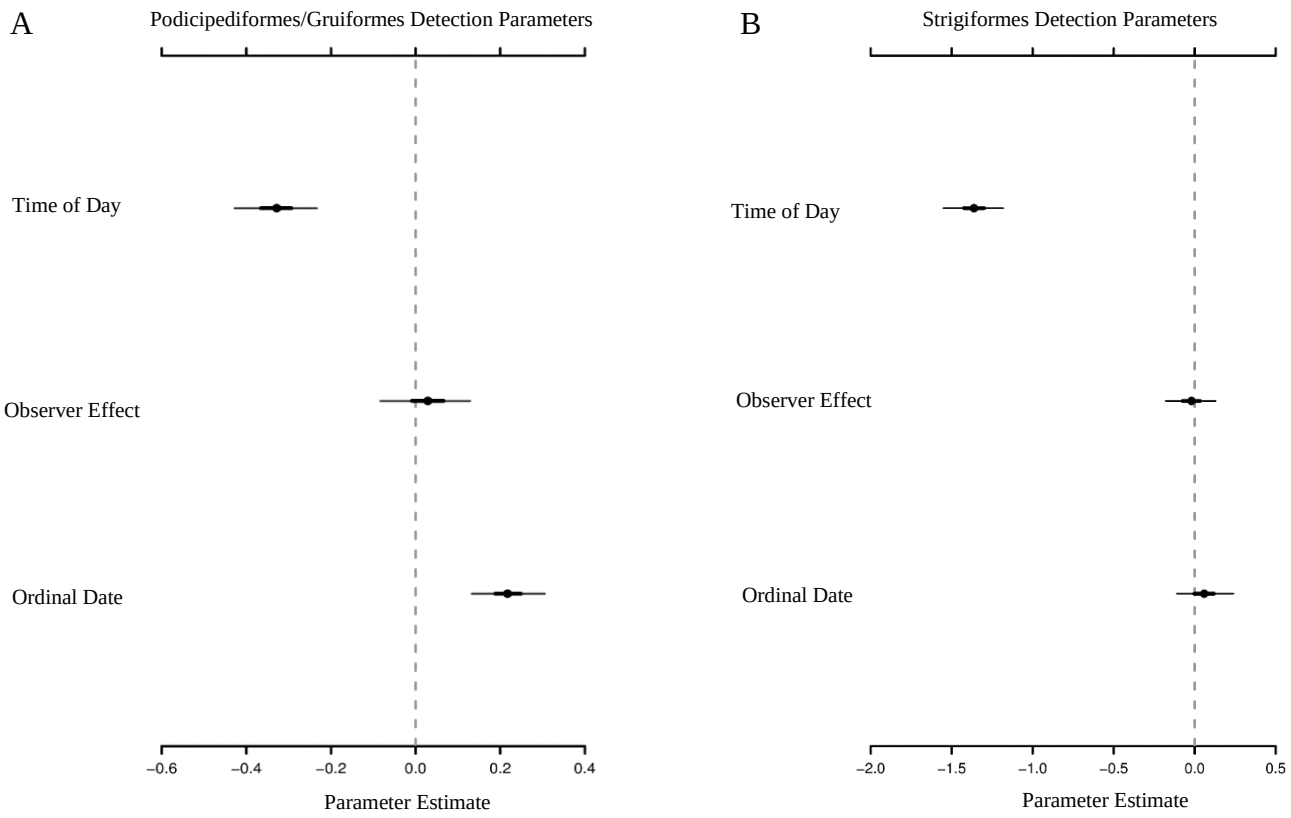

Figure 18. Example of dot-whisker plots for parameter estimates of relevant parameters in detection sub-model used in the multispecies occupancy model. Parameter estimates are plotted relative to zero, including credible intervals for (A) Podicipediformes/Gruiformes (Grebes/Rails) and (B) Strigiformes (Owls) phylogenetic groups.

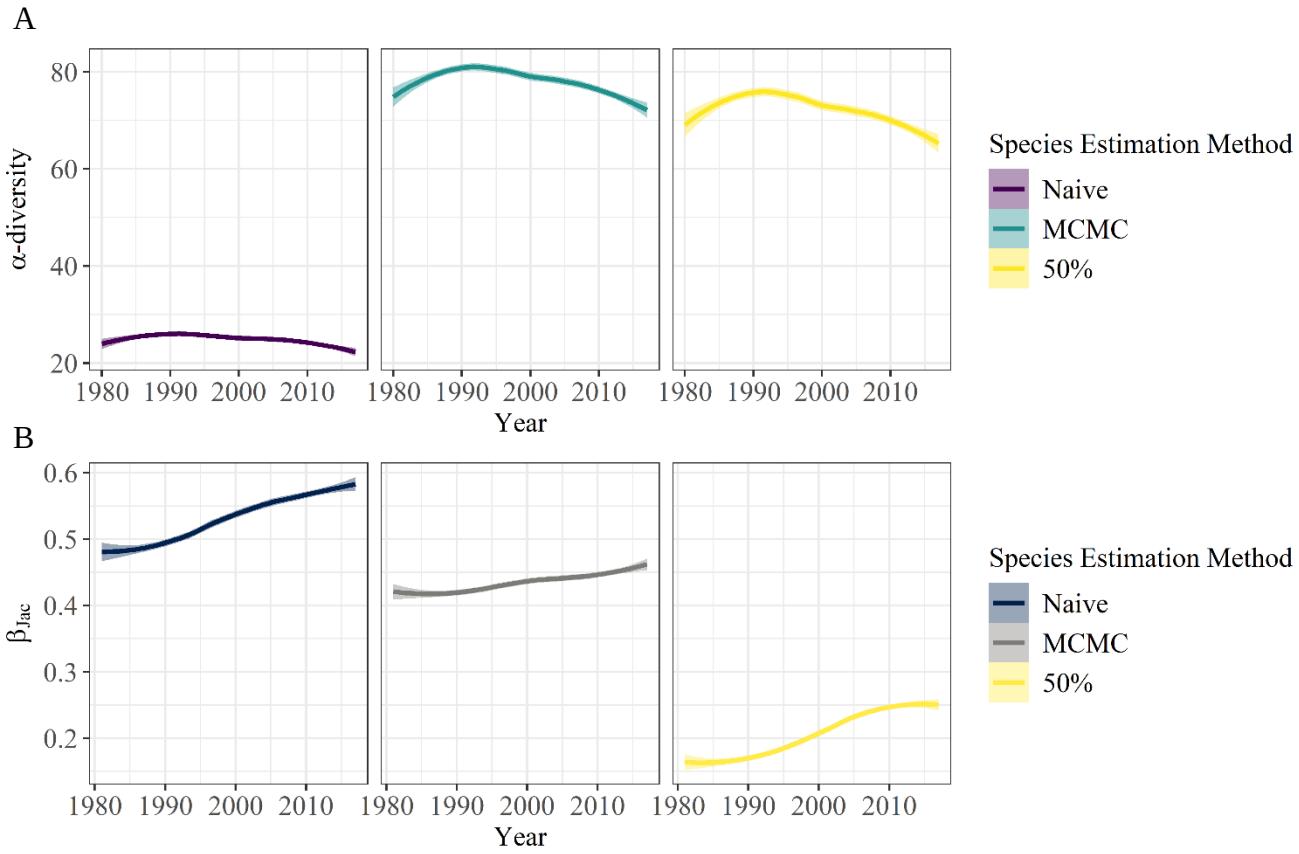

Figure 19. Plots representing (A) change in α-diversity and (B) temporal β-diversity between three estimates of diversity using raw data (Naïve), the last 100 iterations of the MCMC chain, and 50% cut-off for species occupancy.

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